Coevolution in Complex Networks

Gilbert, A.J.

2006

document version
Publisher's PDF, also known as Version of record

Coevolution in Complex Networks

an analysis of socio-natural interactions for wetlands management

Alison J. Gilbert

This dissertation forms part of the research programme, “Wetlands in the Randstad”, financed by the Vrije Universiteit of Amsterdam under its USF-stimuleringsprogramma ‘toponderzoek’.

ISBN: 90-5192-029-6

Cover design: Hans van Herwijnen en Ingrid Constance van der Stelt, beeldend kunstenaars

Press: PrintPartners Ipskamp B.V.

VRIJE UNIVERSITEIT

Coevolution in Complex Networks

an analysis of socio-natural interactions for wetlands management

ACADEMISCH PROEFSCHRIFT

ter verkrijging van de graad Doctor aan
de Vrije Universiteit Amsterdam,
op gezag van de rector magnificus
prof.dr. L.M. Bouter,
in het openbaar te verdedigen
ten overstaan van de promotiecommissie
van de faculteit der Aard- en Levenswetenschappen
op donderdag 2 november 2006 om 13.45 uur
in de aula van de universiteit,
De Boelelaan 1105

door

Alison Jean Gilbert

geboren te Toowoomba, Australia

promotoren: prof.dr. N.M. van Straalen
prof.dr. H. Verbruggen

For Ron
Rick
Kyri

"He'd never been any good at art, and this is a distinction quite hard to achieve in many educational systems. Basic artistic skills …
… are part of a wizard's early training, yet in Rincewind's fingers chalk broke and pencils shattered. It was probably due to a deep distrust of getting things down on paper when they were doing all right where they were."

"The Last Continent" by Terry Pratchet, p 386

Acknowledgements

This dissertation is about interaction, specifically about types and patterns of interaction. While it is largely the product of self-interaction and uni-directional interaction with my computer, there have been quite a number of more interesting, mutual interactions. These interactions have provided me with food, food for thought, an intellectual habitat, and even niche construction when I found myself in the pits of PhD blues. I would like to acknowledge other nodes in the network of interactions that have helped produce this dissertation.

The Vrije Universiteit (VU), specifically its USF-stimuleringsprogramma 'toponderzoek', is gratefully acknowledged for providing financial support.

A dissertation is not possible without supervisors. Prof. Nico van Straalen and Prof. Harmen Verbruggen, like top predators in a food web, have provided top-down control, constraining me from expending my energy in too many directions, guiding me towards a single, specific outcome, yet providing me with the freedom to find my own way. I must confess to having exposed them to resource limitation, a form of bottom-up control in food webs. I would like to thank them for their humour and patience in enduring this.

My supervisors brought very different yet complementary expertises to our three-way interaction. Nico, you have an intellect that can expand in new directions. Thank you for having understood and contributed to my ideas even when they were not fully formed in

my head, and certainly not succinctly explained on paper. Your ability to motivate me and to provide positive feedback when I wrote rubbish (quote “I’m sure I didn’t say it quite like that” unquote) has been impressive. Harmen, you have struggled valiantly with a dissertation topic far from your economics home ground (quote “Ja, dat zal wel” unquote). Your most valued contribution has been to encourage ‘robustness’ in my work, in the more conventional sense of this word and perhaps also in the sense used in this dissertation.

Inspiration has come from many nodes. The notion of coevolution between natural and social systems became clear to me during the ECOWET project. Dr. Ad Barendregt, Prof. Jeroen van den Bergh and Prof. Kerry Turner share responsibility for this, although not for my interpretation.

The direction that my research has taken derives from two papers co-authored by Dr. Jennifer Dunne. Her analysis of food webs, and particularly the correlation between robustness and connectance, was a primary source of food for my thought. She converted this uni-directional interaction into a mutual interaction by providing me with the feeding data for the two food webs used in Chapters 5 and 6 and, in part, in Chapter 7. I gratefully acknowledge this contribution.

Inspiration also derived from the intellectual network provided by the Institute for Environmental Studies (IVM). The network of interactions among the more than 100 nodes comprising IVM is complex, and I would very much like to construct its degree distribution, calculate its connectance, and experiment with adding and removing nodes. Clearly some nodes have been more instrumental in my research than others. While I thank all my colleagues at IVM for services ranging from light entertainment to long and detailed discussions, I would like to thank the following in particular: Jan Vermaat for his ecological support and knowledge of mangroves; Marieke Eleveld and Joyeeta Gupta for proof-reading; and last, but by no means least, Paula Asperen for reformatting and tidying up my figures.

Missing from my thanks to nodes from my intellectual network is someone who is also instrumental in my emotional and social network. Ron Janssen was part of the team that wrote the original proposal to the VU’s USF stimuleringsprogramma. As my partner and father of my children, he has also been a major force in my niche construction at home as well as at work. The ways in which he has supported me during the writing of this dissertation are innumerable. Ron, you have been my guide, my wailing wall, my anchor and my haven. Thank you.

Table of Contents

1. Introduction

"The presence of those seeking the truth is infinitely to be preferred to the presence of those who think they've found it."

"Monstrous Regiment", Prachett 2003, p192

1.1 Coevolution illustrated

A simple illustration of coevolution, and how it impinges on environmental management, is provided by the black-tailed godwit (*Limosa limosa*; see Figure 1.1). The godwit is a migratory bird that breeds in meadows. It has become the symbol of Dutch meadow birds, populations of which tend to be declining. The godwit has Near Threatened status in the 2006 IUCN Red List. Meadow birds are a part of the Dutch polder landscape, a product of some eight centuries human occupation of the Netherlands and of considerable historical and cultural importance to the Dutch. This landscape comprises villages and farmhouses, dairy cows and livestock, meadows intersected by ditches, and 'naturally'-occurring species such as flowers and meadow birds. The polder landscape, and particularly its naturally-occurring species such as the godwit, are a product of coevolution between natural and social systems.

The godwit is dependent on open grassland both foraging and breeding. Populations in the Netherlands are a direct result of human settlement, which drained the predominant fen or bog ecosystems and replaced them with pastures. Initially coevolution was a habitat-mediated interaction between godwits and farmers. Godwit populations reached their peak sizes in the 1950's-1960's but have since been declining. A number of causes have been identified, such as predation by foxes and urban expansion, but a key factor appears to be a change in agricultural practices.

*Figure 1.1 The black-tailed godwit (*Limosa limosa*) (photo courtesy of Mark Kuiper)*

Fertilizers and improved pasture species cater for faster grass growth so that it can be mowed earlier in the season. Early mowing as well as high stocking rates destroys many nests. Godwit beaks are long, adapted to finding food in the moist soil. Management of groundwater levels combined with the homogenous nature of modern pastures mean less food availability. The human activity that created conditions favouring the godwit has come to threaten its survival. Coevolution of godwits and farmers has taken a new course.

Nature conservation groups highlight the population's decline. Efforts are being made to conserve and restore populations. Policies have been implemented to change the timing and manner in which meadows are mowed to increase nestling survival. Such measures generate costs, or foregone benefits, to farmers, although subsidies pass the costs on to society at a whole. Godwit conservation has entered the debate about fox hunting, with proponents arguing that this sport reduces fox populations and so predation pressure on godwits.

Few members of Dutch society remain untouched by this environmental issue, if only to the extent that their tax euros are spent on conservation efforts. However, there is no guarantee of success. An economic perspective on godwit conservation would assess whether conservation costs are balanced by the social benefits of godwit survival. By promoting and conserving godwit habitat, the ways in which social systems use land changes. Land provides space for agriculture and infrastructure. Changes in agricultural practices, habitat restoration by environmental NGOs, constraints on urban expansion, and other measures engender costs. These costs can be traded-off against the benefits of godwit survival, including indirect use values, e.g. recreation, and non-use values.

A coevolutionary approach would highlight the changing nature of interaction between godwits and the social system, and the changing role of godwits within natural systems. What initially was a one-to-one interaction between godwits and farmers, now embroils much of Dutch society, including environmental NGOs, bird watchers and foxhunters. Some of these interactions have developed gradually, over the last hundred or so years, while others derive from the recent decline in godwit populations. Farmers are affected by policies influencing pasture management and by changes in water management, required to restore soil ecosystems and generate sufficient forage for godwits. Predation by

foxes has been a contributor to population decline, but foxes have shown themselves particularly difficult to eradicate. With or without fox hunting, the godwit's future is likely to include depredation by foxes. The godwit also competes with other species for food and nesting sites. Competitive balances are likely to have changed, either as a result of changes in godwit populations or as a result of more general environmental impact. Finally, the godwit is a migratory species. While breeding success in the Netherlands is necessary for its survival, the species is also dependent on other ecosystems throughout Europe. Conservation measures may be needed to restore or maintain its winter and migration habitats, implying a large set of natural and social systems and interactions.

A coevolutionary approach would assess how these trends within both systems are likely to extend into the future, how this will affect future interactions between systems, and how system components might subsequently adapt. Will both systems be able to support a recovering godwit population? What would the extinction of godwits mean for both systems? Which social actors, ecosystem components and system processes would be affected? Would other system components be placed at risk, or profit from an absence of godwits? How would such effects filter through both systems and their interactions? Might system stability be adversely affected? How will this affect future interaction between the two systems, and particularly future interaction to the benefit of human society? While such questions place a considerable burden on the godwit, human settlement of the Netherlands has led to other instances of coevolution. The questions also highlight that coevolution is part of the sustainable development debate, depicted in Figure 1.2. The figure at the top represents an economic perspective on the interaction between natural and social systems. The figure at the bottom highlights the central concern of sustainable development, that present societies are consuming so much natural capital that choices for development by future generations will be severely constrained.

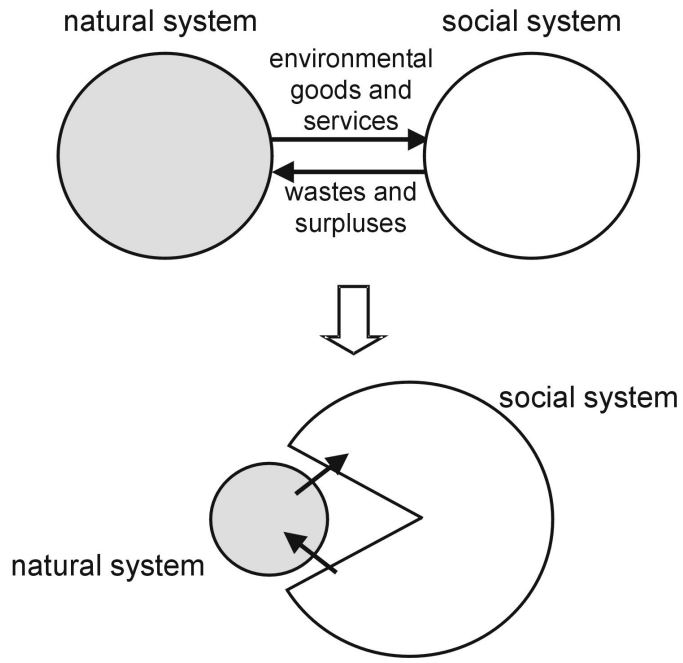


Figure 1.2 Interactions between natural and social systems; the sustainable development debate raises concerns that we are consuming natural capital to the detriment of future generations

At the heart of sustainable development is the understanding and management of how natural and socio-economic systems interact. Management actions include pollution abatement (reducing the volumes of wastes and surpluses entering natural systems), quota on fish catch (reducing the consumption of environmental goods), establishment of national parks and ecotourism (management of our consumption of environmental services), to reduce the pressure being placed on natural systems. Coevolution emphasises the reciprocal effects of interaction between two systems. The farmer drains land to create pastures. The godwit breeds in the pastures and becomes a symbol of Dutch agricultural landscapes. With declining populations, Dutch society, concerned by the loss of cultural values, institutes conservation measures.

My dissertation develops a method, termed topological network analysis, for analysing coevolution. Central to my method is the multiplicity of interactions among components of natural and social systems. These interactions lie behind component (e.g. population) dynamics, component evolution, coevolution among components, and emergent system properties. Interactions are represented as a complex network. I develop a criterion – change in robustness – that allows comparison of alternative interventions into ecosystems. Robustness is defined in terms of secondary loss of network components and fragmentation of networks. This definition suggests two indicators for robustness. I develop a third indicator, change in connectance, which captures changes in the pattern of interaction among network components.

The illustration above sets the scene for my dissertation. The remainder of this chapter introduces key terms, presents objectives and approach, outlines the structure of the dissertation, and bounds its subject matter and the scope of the method being developed.

1.2 Coevolution of complex networks

1.2.1 Coevolution

This dissertation draws from a number of disciplines. Different disciplines adopt their own terminology and may even use the same words but with different meanings. The glossary at the end of this dissertation offers definitions of many terms that will be encountered. Disciplines may also have precise meanings for words that also in common use with a more general meaning. While our current understanding of evolution began with Charles Darwin's *The Origin of Species*, the word pre-dates Darwin (Hodgson, 1993 in Nelson 1995). Non-specialist dictionaries do not distinguish among evolution, growth, change, development and progress, while most scientific use of evolution does.

Darwin viewed evolution as the descent of organisms with modification in form, physiology or behaviour over generations (Ridley 1996). After much discussion, evolutionary biology has come to recognise three mechanisms driving evolution. Two of these, genetic drift and gene flow, involve neutral evolution, which may have no effect on fitness. Darwin identified the third, natural selection, as the mechanism by which organisms adapt to their environment and so evolve. There is a long history of recognition that organisms are well-adapted to their environments but, prior to Darwin, the mechanism was believed to be the direct action of God. The controversy that Darwin triggered was to explain adaptation in a way that did not involve divine intervention.

The modern view of natural selection argues that it is triggered by interactions among species and between species and their physical environment. Adaptation to another species, unlike adaptation to the physical environment, can produce reciprocal evolutionary responses. Reciprocal evolutionary change is coevolution. An easily recognisable example of coevolution is provided by flower shape and colour, and the mouthparts and sensory perception of their pollinators (Barth 1991, Labandeira *et al*. 1994 – see Figure 1.3). Evolutionary biologists first defined the term in the 1960's (Ehrlich & Raven 1964). Coevolution is now seen by evolutionary biologists as an umbrella term for a variety of processes and outcomes of reciprocal evolutionary change (Thompson 1994).

Figure 1.3 Flower shape has coevolved with the mouthparts and sensory perception of their pollinators

The term coevolution has found a place within the sustainable development debate (Norgaard 1984, 1994; Gowdy 1994, Bergh & Gowdy 2000; Rammel & Staudinger 2002; Rammel & Bergh 2003; Bergh & Stagl 2003; Winder *et al*. 2005; and Norgaard 2005) and in some aspects of environmental management (e.g. Gadgil & Berkes 1991; Colding & Folke 1997). Use of evolutionary terminology emphasises the long time horizon needed to assess the full implications of current societal activity. It also serves to highlight the complex and dynamic nature of interactions within and between systems, their influence on system states, and that some system components may survive better than, or are selected over, others.

Of particular interest to this dissertation is the potential for the effects of interaction between natural and socio-economic systems to rebound on each other, as is elucidated in the following quote (Lorenzoni *et al*. 2000a, p57-58 and citing Norgaard 1984; Norgaard 1994; Turner *et al*. 1998; Adger 1999) and illustrated in Figure 1.4:

> *"[Coevolution] emphasises that social structures and their processes impinge on the environment, thus modifying and changing it. Such changes in turn shape the structure of social systems, which subsequently undergo further changes in order to be better positioned to adapt to the changing environment. The interaction between systems is constant and reciprocal. A 'co-evolutionary' approach highlights the complex coupling of the two systems now and into the foreseeable future*".

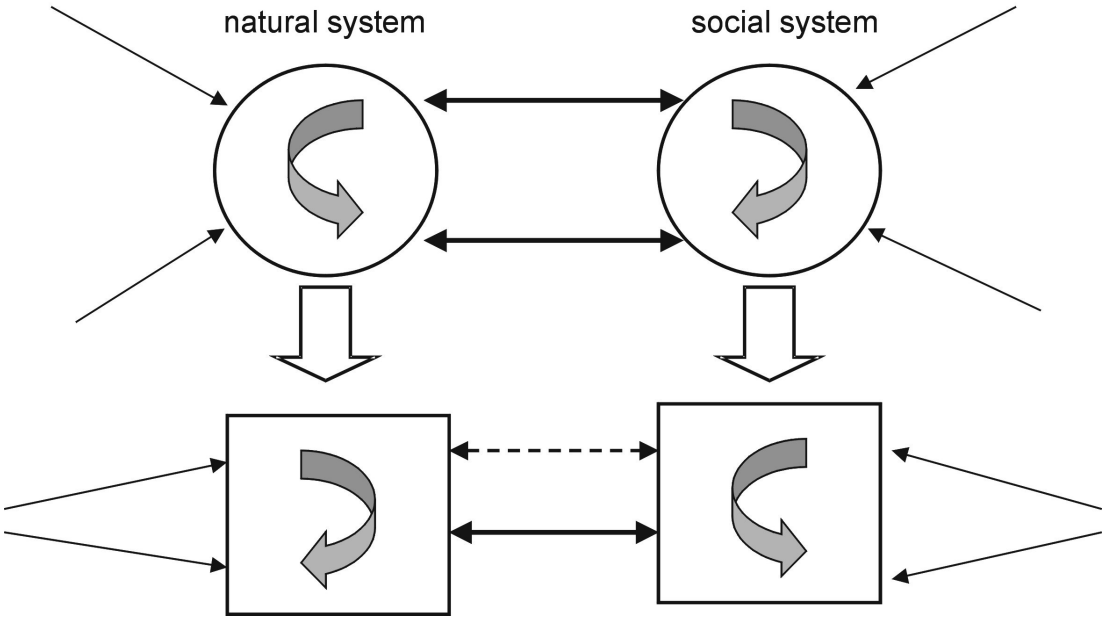


Figure 1.4 'Coevolution' of a natural and a socio-economic system as elucidate by Lorenzoni et al. *(200a); coevolution is indicated by change in system state (round to square), change in internal processes (direction of curved arrows), and change in system interaction (different arrow thicknesses)*

Winder *et al*. (2005) argue that distinction should be made between coevolution and co-dynamics. Populations of species can exhibit co-dynamics, such as the well-documented oscillation in snowshoe hare and Artic fox populations, without leading to adaptive change. Winder *et al*. identify three necessary ingredients for an evolutionary perspectives: the existence of an entity capable of continued existence; diversity of attributes and mechanisms that promote this diversity; and stress, which winnows diversity and leads to selection of fitter attributes.

While evolutionary biology is the origin of the term, its use in the sense of coevolution between natural and social systems draws heavily from the study of complex systems. Stuart Kauffman (Kauffman 1993) offered the following hypothesis for coevolution (p261 – elaborated further in Chapter 4):

> *"…., organisms adapt under natural selection via a* metadynamics *where each organism myopically alters the structure of its fitness landscape and the extent to which that landscape is deformed by the adaptive moves of other organisms, such that…. the entire ecosystem coevolves to a poised state at the edge of chaos."*

He argues for the existence of an attractor, providing quasi-stable conditions, and of small and large, endogenously-driven avalanches of speciation and extinction events in ecosystems. Similar notions are implicit in Holling's adaptive cycle (Holling 1986; Gunderson *et al*. 1995), which describes the progress of systems through growth, collapse and reorganisation. Coevolution in complex systems emphasises two aspects. Firstly, interacting system components are subject to processes selecting how well they 'fit' together. Secondly, changes in system composition and/or the pattern of interaction could disrupt coevolved equilibria and lead to system breakdown and reorganisation.

1.2.2 Adaptation

While not in the dissertation's title, adaptation goes hand-in-hand with evolution and is a term that has also found its way into environmental management. In evolutionary biology, an adaptation is defined as a feature, character, trait enabling an organism to survive and reproduce better in its natural environment, than if it lacked this feature (Ridley 1996). Adaptation may also be defined as the process by which organisms become adapted (e.g. Futuyma 1998). An adaptive trait confers reproductive advantage on the individual possessing it relative to others that do not. Much research in evolutionary biology tries to explain how organisms have adapted, to demonstrate how a particular trait is adaptive, and whether natural selection is driving adaptation. Evolutionary biologists are satisfied that natural selection is the only mechanism driving adaptation. However, care is needed in explaining why a particular trait is adaptive, as shown in Box 1.1.

Box 1.1 Hypotheses explaining the adaptive white pelt of the polar bear

Polar bears are unique among bears in being white, a trait that would seem to be adaptive since they probably evolved from a brown ancestor. What is the selective advantage of a white coat? Polar bears live in the arctic, where they spend much of their time silhouetted against a snowy background. The camouflage hypothesis suggests that being white on a white background would help in hunting of seals.

The hunting strategies of 288 polar bears were recorded to test the camouflage hypothesis (Stirling & Archibald 1977): sneak and pounce – one bear; jump and crush– 54 bears; sit and wait – 233 bears. The sneak and pounce strategy is the only strategy consistent with the camouflage hypothesis; sitting and waiting in ambush does not require camouflage.

Polar bears photographed under UV light are black, indicating that the pelt absorbs UV light. Examined closely, the individual hairs are not white but clear, lacking pigment found in most other mammals. The possibility that the hairs' function is to trap incident light and reflect it back towards the animals skin leads to a solar heat collector hypothesis. Tributsch *et al*. (1990) showed that solar irradiation may change subcutaneous temperatures by as much as 10°C as a result of the energy transparent pelt.

The polar bear's skin could be a kind of sensory system, using the temperature pattern produced on its surface by scattered light. This led to yet another hypothesis, the navigation hypothesis. Temperature patterns may help bears to determine the approximate position of the sun, to navigate under diffuse arctic visibility, and also to locate ice-free sea surfaces where the scattering of light is significantly reduced compared with ice-covered surfaces.

A neutral hypothesis is also possible. The white colour could stem from a mutation in the pigment-producing pathway. Persistence of the colour could simply indicate that the mutation does the bears no harm.

Evolutionary biology is predominantly a backward-looking science, attempting to explain how past evolutionary processes forged species' characteristics. Its capacity to predict future evolution is limited by our ability to answer three fundamental questions: which selective pressures are most crucial to a given species' survival? to what pressures is a species capable of adapting (encompassing issues of phenotypic plasticity)? what is the interplay between adaptation and ecological processes that also play a role in a species' survival? This dissertation does not attempt to specify or predict future evolution or coevolution of a species. Its evolutionary perspective focuses on species extinction, or the inability of species to adapt to changing circumstances, and subsequent system-wide effects.

Both ‘adaptation’ and ‘adaptive’ are words used in environmental management. While their use draws on evolutionary biology, it may not abide strictly by evolutionary biological definitions. Use may emphasise different aspects of adaptation, as illustrated by two examples: adaptive management and adaptation strategies.

Adaptive management has been defined and interpreted in a variety of ways such as: social sciences (Argyris & Schön 1978); business management (Senge 1994); professional practice (Schön 1983); ecosystem management (Holling 1978; Walters 1986; Gunderson *et al*. 1995; Lee 1993); and conservation practices (Margoluis & Salafsky 1998). In the last two, adaptive management emphasises interaction between science and policy, a ‘learning by doing’ or experimental approach to management, and uncertainties in our knowledge of how ecosystems function. It is characterised by a systematic process of modelling, experimentation, and monitoring to assess management actions. Multiple management policies are applied following a rigorous experimental design that allows scientists and managers to compare ecosystem response to alternative management strategies.

Adaptive management has been developed independently of evolutionary theory and, in sharp contrast to this theory, looks forwards not backwards. It tests for the most appropriate management paths, much as natural selection tests for the fittest phenotypes. Adaptive management both promotes variability in management alternatives, and selects from this variability for the more promising.

Another use of adaptation may be found in describing strategies to adjust to climate change. The International Panel for Climate Change defines adaptation as: “adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities” (IPCC 2001 p72). This definition draws on evolutionary theory with its gradual shift in phenotypes that may occur in response to environmental change. It emphasises accommodation of change, rather than combating it, or trying to prevent it. As with adaptive management, this use of adaptation does not relate explicitly to natural selection, although it implicitly argues that employing strategies that reduce harm from, or exploit opportunities created by, climate change will confer a survival advantage. It does not explicitly address associated selection and, as with adaptive management, is forward-looking,

The thinking behind adaptive management and adaptation strategies is also reflected in the notion that natural and social systems coevolve. ‘Coevolution’ is most definitely forward-looking. It poses questions as to the repercussions of systems’ interaction, the kinds of selective pressures generated, how system components might react and which reactions will be more successful.

1.2.3 Complex networks and socio-natural interactions

Interaction is a necessary precursor of natural selection and subsequent evolution and so is a central theme in this dissertation. Specifically, interactions among components of social and natural systems, termed socio-natural interactions, are addressed. Interactions among components of complex systems may be captured as a network comprising nodes and links. Nodes or vertices are system components; consider authors in a citation network or species in a food web. Links capture interactions between nodes, such as author

a cites author *b* or species *a* eats species *b*. A complex network is the product of past coevolution among complex system components. Coevolution engenders an image of jockeying and jostling as different combinations of components, interactions and interaction strengths are tested for their ability to 'fit' together. A network provides a snapshot of one instance within the growth, development and evolution of a system as a whole, as well as providing the template for future coevolution.

Disordered or 'real world' networks have recently been receiving much attention as models describing the interactions among components of complex systems. Real world networks have been shown to be neither regular lattices, where nodes are connected according to a specific pattern, such as the molecules in a crystal, nor random graphs where nodes are randomly connected to other nodes. However, they tend to have some topological characteristics in common, such as a small number of links separating nodes and the frequency distribution of nodes and links. Real world networks often have many poorly-connected nodes but only a few highly-connected nodes or hubs. Experiments removing nodes from networks have shown that such topological features convey robustness when nodes are randomly lost whereas the loss of hubs can have far reaching consequences, such as the secondary node loss and fragmentation of the network.

Recent years have seen a merging of this new research focus with more traditional research into food webs. Food webs map feeding interactions among the members of an ecological community. Feeding interactions are a major source of natural selection. Ecosystems are an example of a complex system, and food webs are one type of complex network. From the limited number of food webs investigated so far, they would seem to have different topologies than other real world networks, and that these topologies that might make them less vulnerable to hub loss. Much more research into food web topology and how topological patterns emerge can be expected in coming years.

As an ecologist, I focus on the natural system, notably ecosystems. Evolutionary and coevolutionary perspectives on social systems are not treated. Sethi and Somanathan (1996), Janssen (2002), Noially (2003), Penn (2003), Janssen and Ostrom (2005), Bergh and Stagl (2003) and Bergh *et al*. (2006) provide an introduction to this literature. Food webs, as complex networks and as one representation of interactions among the components of ecosystems, are the source of inspiration for the method developed in this dissertation. Much conventional food web research omits the human species, even though the structure of many, if not most, food webs is strongly influenced by human activities. Not only have we been historically a part of food webs but also our more recent impacts on ecosystems are causing loss of biodiversity and homogenisation of ecological communities at a global scale. This could have potentially dire consequences for the structure, function and stability of ecological communities, both now and in the future, and so on the nature and strength of future socio-natural interaction.

1.2.4 Wetlands

Among the many ecosystems being adversely affected by human activities, my dissertation emphasises wetlands and particularly mangroves. Wetland ecosystems are located on an ecotone, or gradient, between fully terrestrial and fully aquatic environments. They

can be very species rich and very productive, suggesting an ecological community with a complex set of interactions.

Wetlands have been frequently perceived as derelict or wasteland that contributes little to society except mosquitoes. Large tracts have been converted to other land uses such as agriculture, aquaculture, ports and harbours. Recent decades have highlighted the indirect benefits, largely environmental services, that wetlands contribute to social systems. These include nursery habitat for commercial aquatic species, water purification, and habitat and feeding grounds for charismatic and migratory species. It is also now more widely recognised that human communities operating on a subsistence or traditional basis often make extensive use of species found in mangroves. Mangrove products include wood and leaves for construction and fuel, edible species, and flowers, fungi etc used to prepare traditional medicines.

Much effort is now being undertaken to conserve wetlands. This is despite often considerable pressure for their conversion, as illustrated by the dissertation's case study dealing with mangrove conversion to fishponds. The United Nations Environment Programme (UNEP-WCMC 2006) has recently brought the importance of mangroves into even sharper focus. The report underlines the vital role mangroves play in stemming coastal erosion, providing nurseries for fish, and absorbing the energy of wind-generated waves. The report argues that conserving mangroves is a small price to pay when set against the costs of destroying them or substituting their role with man-made structures.

1.3 Research approach

1.3.1 Systems analysis

Problems beg solutions. Solutions to environmental problems, either repairing current or preventing future damage, are frequently compromised by a multiplicity of objectives to be realised, such as the hip pocket nerve, save the whale, not in my backyard, and the diversity of interests at play, such as farmers, conservationists, the public at large. Many 'solutions' to environmental problems can be envisaged. For example, we can mitigate greenhouse gas emissions to tackle global warming and reduce sea level rise. Or we can reinforce coastal defences to keep out the sea. Or we can build our houses on stilts and buy boats instead of cars. The most viable solution is frequently not clear.

Systems analysis has a variety of meanings. In the context of this dissertation, it refers to a technique that helps a decision-maker identify a better course of action and make a better decision than he might otherwise have made. At its most basic level, systems analysis comprises three steps: identify alternative actions; simulate these alternatives, usually with the use of a model; and, rank the alternatives according to their performance. In more elaborate versions, iteration, interaction with policy-makers and other stakeholders, and scenarios may be added.

The above three steps may be seen in cost-benefit analyses, where the second step values the costs incurred and the benefits expected from different actions, and the third step identifies the most profitable action. Gilbert and Janssen (1998) followed this approach by estimating the value accruing to different interventions in the Pagbilao mangroves. Problems with valuation and recognition that economic efficiency is not the only crite-

rion relevant for decision-makers have lead to more elaborate models and to additional evaluation criteria. For example, Janssen and Padilla (1999) used the same information in Gilbert and Janssen (1998) but applied three evaluation criteria: economic efficiency, environmental quality and social equity. Similar criteria have been used to assess nutrient abatement in the River Rhine catchment (Veeren & Lorenz, 2002; Salomons 2004) and changes to land use in the Vecht River floodplain (Gilbert *et al*. 2004).

These, and other studies, show that environmental and economic goals frequently conflict. What is good for the environment tends to cost too much, and what is good for the economy tend to cause environmental degradation. Trade-offs between economic and environmental goals are subsumed in my analysis. A single criterion is applied, relating to the continued robustness of the social-natural network representing interacting social and natural systems. The relevance of this criterion to decision-makers lies in their presumed desire to avoid a regime shift given uncertainties as to which system components will survive to reorganise into what kind of state.

1.3.2 Research objectives

The goal of this dissertation is to develop the means for comparing different human interventions into ecosystems with regards to their impact on the future coevolution of interacting natural and social systems. The term 'human intervention' is used in preference to environmental management. The latter term implies care for the environment, whereas human intervention includes other interests, such as making a profit. My specific research objectives are to develop the two elements comprising such means, namely:

1. a method that simulates the impact of intervention on coevolution; and,
2. a criterion and indicators for comparing the impact of different interventions.

The method is termed topological network analysis, and indicates my focus on the topology – number and pattern of interactions – of complex networks. Topological network analysis contrasts with functional analysis, which considers not only the structure but also the dynamics, such as the rate at which components exchange materials, of the network. A socio-natural network integrates interactions within and between a natural and a social system. Topological network analysis assesses the impact of human intervention on the topology of such a network. A predation matrix is used to represent interactions that result in the transfer of matter and energy between pairs of system components. Different interventions are translated into changes in the risk of species' extinction. Per alternative, both the number and which species become extinct as a result of human intervention are specified and subsequently removed from the network.

By causing species loss and the loss of associated interactions, intervention changes a socio-natural network's topology. These changes are interpreted in terms of their impact on network robustness, which is the criterion for comparing the different interventions. Robustness is defined in the literature in terms of secondary node loss and network fragmentation. As one of a number of stability concepts, it addresses the ability of networks to resist the breakdown of their internal connections. Such a breakdown can lead to a regime shift as a system moves from one state to another. Secondary node loss and fragmentation are clearly two indicators of robustness. I develop a third, change in connectance.

Topological network analysis addresses coevolution in three main ways. Firstly, its representation of interaction captures a system's structure and changes in that structure following human intervention. Changes in structure could presage a regime shift. Secondly, topological network analysis focuses on the extinction of system components, which occurs when components are not able to adapt quickly enough to changing conditions. Finally, topological network analysis comprises the requisite components identified by Nelson (1995) and Winder *et al*. (2005). Firstly, a socio-natural network comprises entities capable of continued existence. Secondly, the network represents current diversity and the human interventions, by introducing new economic activities, represent sources of increased diversity. Thirdly, this increase in diversity is winnowed by the differential impact on components' extinction risk. Finally, while topological network analysis is a tool for simulating the future, it does not predict future adaptation. The networks, representing the current condition and the condition after human intervention, should be seen as the template for future co-dynamics and coevolution.

1.3.3 Structure of the dissertation

Seven research steps, corresponding to Chapters 1-7, are followed (see Figure 1.5).

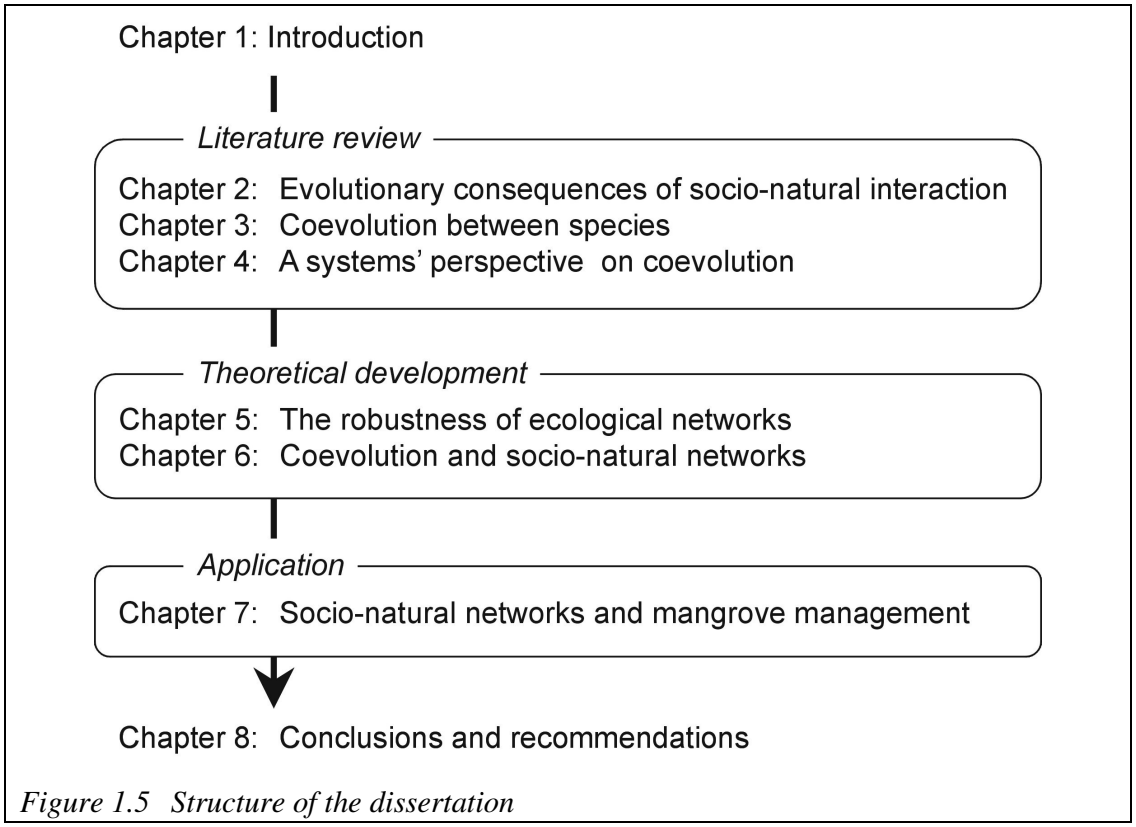


Figure 1.5 Structure of the dissertation

The first step, undertaken in this chapter, provides the context of the research problem, specifies research objectives, and bounds the research activity. The next three steps, in Chapters 2-4, review relevant literature. Step 2 examines interactions between social and natural systems, emphasising the impact that social systems have on ecosystems. Interactions are grouped into four broad types and their ecological and evolutionary consequences discussed. Much concern about the future of natural systems lies with the loss of

biodiversity. Current knowledge about the relationship between biodiversity and ecosystem stability is summarised and a selection of stability concepts are introduced.

Step 3 reviews the literature on coevolution from evolutionary biology, where the term originates. Interactions between species are classified and (co)evolutionary responses to interaction are summarised. Much discussion about coevolution emphasises escalation in the interaction, via such terms as 'evolutionary arms' race' and the 'Red Queen hypothesis'. Escalation maintains, even exacerbates, antagonism between two species. However, my review shows that other courses are clearly evident in inter-species interactions, and draws parallels for the management of socio-natural interaction.

Step 4 upgrades the perspective, from interaction between two species to interactions among the components of complex systems. There is a large body of literature on this subject and, apart from a general introduction to the topic, I focus on environmental and ecological perspectives. For example, the adaptive cycle proposed by Crawford (Buz) Holling to explain the progress of systems through phases of growth and decline is rooted in complex systems' thinking. The chapter reinforces my emphasis on interaction, and comes to focus on networks of interactions as the backdrop against which evolution and coevolution occur. It also introduces issues of network topology and robustness. Recent research combining complex networks and food webs form the basis for the development of my method.

Theoretical development of both method and criterion occurs in the next two steps, in Chapters 5 and 6. These steps combine different elements from the literature review to develop the method and specify the criterion and its indicators. Step 5 leads directly from the combination of complex networks and food web analysis reviewed at the end of Chapter 4. Recent research shows that network robustness is correlated with connectance and so with the topology of complex networks. Step 5 examines the behaviour of connectance as an indicator of the robustness of a network. I use two food webs from the literature, with interactions represented in the form of a predation matrix. Nodes, in this case species, are removed according to various removal protocols. The basic mechanics of my method are illustrated in this step.

Step 6 expands on the nodes being removed and on the type of network being considered. Node removal protocols used in Step 5 are based on network features, notably how connected they are, and not on extinction risk. Step 6 returns to the four categories of socio-natural interaction identified in Step 2 to estimate the network features of species under threat from social impact, and the effect on food webs of their loss. Socio-natural interactions comprise a variety of interaction types, both within ecological (e.g. competition, cooperation, niche construction) and economic communities (e.g. exchange of goods and services) as well as between species and human activities (e.g. habitat degradation, extraction, aesthetic appreciation). A food web captures only interactions that transfer matter and energy through an ecological community. Step 6 considers other types of ecological interaction, as well as how interactions among components of economic systems, as one example of a social system, are documented. This step justifies the choice for using the predation matrix to represent a socio-natural network.

Step 7 applies the method and criterion to compare different interventions into a mangrove stand in the Philippines. These interventions are translated into economic activities

added to and species lost from the socio-natural network. Change to connectance and evidence of secondary nodes loss and network fragmentation are recorded and the alternatives compared in terms of their impact on network robustness.

The final chapter summarises conclusions, recapitulates on the dissertation's storyline, evaluates the dissertation's products, and recommends directions for further research.

1.4 Limitations

I identify four limitations to my approach. Firstly, my method leads to the comparison of alternative interventions according to only one criterion, robustness. As discussed above, a wide range of evaluation criteria may be found in the literature, such as economic efficiency, environmental quality and societal equity. Robustness is not a fourth criterion. It takes an integrated approach towards sustainable development, focusing on interactions between and within social and natural systems and their future coevolution.

The second limitation is that my method focuses on the failure of species (or populations of species) to adjust to changing conditions, and so to be lost from socio-natural networks. This focus is a direct product of viewing the loss of biodiversity as the hallmark of social impact on natural systems, and of extending recent research into network robustness. My method cannot address management issues associated with environmental rehabilitation and ecosystem restoration. It can only be applied where extinction risk is affected to different degrees by different human actions.

Thirdly, my method focuses on the breakdown of connectedness in a network. This can be equated with the 'worst case scenario' for coevolution among a system's components, as it could herald a shift in system state. Breakdown in connectedness is caused by species loss. There are, presumably, many courses that coevolution could take that would not effect such dramatic changes. These are not addressed.

Finally, topological network analysis has no explicit spatial or temporal context. Neither the spatial extent of a socio-natural system, nor the spatial location of components and interactions bears on the analysis. The time over which intervention occurs can be specified, but has no effect on the simulation of its effects. Adverse impacts on a network, notably secondary node loss and fragmentation, may be simulated, but when they occur is not specified. Alternative interventions are compared on the basis of the final state of the network and on the changes it undergoes, not on how long it takes to reach this final state nor when the changes occur.

The following chapter is the first in a block of chapters reviewing relevant literature. It presents a categorisation of socio-natural interactions and identifies their short- and long-term adverse effects. The chapter also introduces a range of stability concepts, and summarises our current knowledge of how biodiversity influences ecosystem stability.

2. Evolutionary Consequences of Social Impact

"Life emerged from the burrows and fissures. Soon, the desert was filled with the buzz and click and screech of creatures which, lacking mankind's superior brainpower, did not concern themselves with finding someone to blame and instead tried to find someone to eat."

"Jingo", Pratchet 1997, p372

2.1 Introduction

Environmental awareness in general, and the debate around sustainable development in particular, have drawn attention to the diversity of interactions between natural and social systems and the adverse impacts that social systems can have on natural systems. Some of these impacts may, in turn, adversely affect social systems. The term 'social impact' is used to denote an interaction between these natural and socio-economic systems that causes a negative effect on the natural system.

I look at natural systems in a particular way. My perspective encompasses the interactions that occur between biotic and abiotic components and among the biotic components, together with the processes underlying mass and energy fluxes. Consequently, I equate ecosystems with natural systems. Social impact is perceived to be a major threat to the survival of many species and the ecosystems that house them. This chapter provides a summary of the impacts that human activities have and have had on natural systems, and the potential evolutionary consequences of that impact. The material in this chapter provides a backdrop for the rest of the dissertation.

The subject of this chapter is illustrated in Figure 2.1. This figure follows the format of the figures introduced in Chapter 1. The living components of ecosystems interact with each other and with their physical environment. These interactions drive ecosystem processes, which are represented by the curved arrows. Some components also interact

with social systems. These diverse interactions drive the evolution of ecosystem components, selecting for those individuals best suited to their environment. This evolution may effect changes to the ecosystem (indicated by the different shading), changes to ecosystem processes (indicated by the different direction of the curved arrow), and, in turn, to the future interactions between the systems (indicated by the different thicknesses of the lines between the systems). The social system also changes. Such changes are not addressed, except generally, because both the chapter and the dissertation as a whole focus on changes to ecosystems.

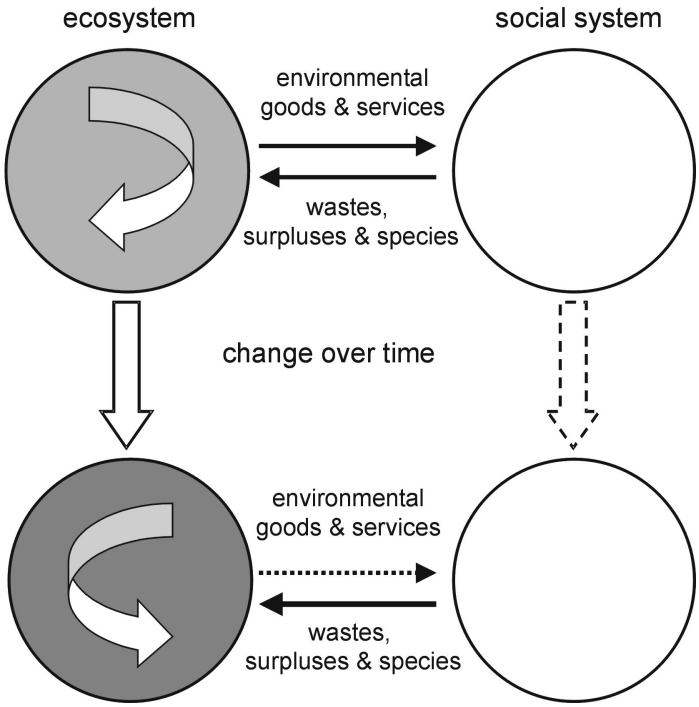


Figure 2.1 Evolutionary consequences of socio-natural interaction for a natural system; evolution may cause change in system components, processes and emergent properties

The human species and its social system use natural systems deliberately to boost production and reproduction. Our phenomenal success at commandeering resources and transforming the landscape has led to environmental impacts at a scale where there are doubts as to the ecological and evolutionary viability of many species and ecosystems (Western 2001). This in turn raises doubts as to whether future natural systems will continue to provide environmental goods and services, and the choice of goods and services available to future generations. The social system has become a, if not the, dominant factor driving evolutionary change in biological systems.

Selective influences are increasing rates of evolutionary processes by orders of magnitude (Palumbi 2001 – see Box 2.1). This is paired with a rate of species extinction that is currently estimated at 50-500 times background rates and increasing (Woodruff 2001). In instances with potential economic consequences, such as resistance to pesticides and antibiotics, we are developing quite sophisticated understanding of the emergence of adaptation, perhaps to the extent of being able to predict the future evolution of select species (Munro 1997).

Box 2.1 Examples of human-induced evolution (references in Palumbi 2001)

Paul Müller's 1939 discovery of DDT won him the Nobel Prize in 1948. Before the ceremony occurred, evolution of resistance had been reported in house flies. By 1990, over 500 insect species had evolved resistance to at least one insecticide. Many species are resistant to so many pesticides that they are difficult or impossible to control.

Insects evolve resistance within a decade after introduction of a new pesticide; weeds evolve resistance within 10-25 years of deployment of an herbicide.

Virtually all Gram-positive infections were susceptible to penicillin in the 1940s. The vast majority of hospital infections (e.g. *Staphylococcus aureus*) come from this group and have evolved penicillin-resistance.

Under heavy fishing pressure fish evolve slower growth rates and thinner bodies that allow them to slip through gill nets.

Invading species, introduced by humans, have been known to evolve rapidly to match local selection pressures.

Introduced predatory fish have caused rapid evolution of life-history traits and colour pattern in their prey fish species (e.g. cichlids in Lake Victoria).

The predominant ecological effect of social impact is loss of biodiversity, a phrase that has captured the imaginations of policy-makers, scientists and the public at large. While an ecological effect, biodiversity loss could very well have evolutionary repercussions. Scientists point to the long recovery times from past mass extinction events, and ask whether we are entering another such event. Biodiversity loss provides a possible link between ecological effect and evolutionary consequence.

This chapter provides an overview of social impact, its ecological and, in particular, its evolutionary consequences. More specifically, it aims to:

- identify the main sources of social impact on ecosystems;
- summarise their ecological effects;
- examine whether a relationship exists between diversity and stability; and,
- assess their evolutionary consequences.

I have classified social impact on the basis for four broad types of interaction whereby human activities have adversely affected natural systems: extraction of select species, disposal of wastes and surpluses, conversion of natural to human habitats, and introduction of species to new locations. Interaction between the two systems is a central theme in my dissertation. This classification leads to four categories of social impact, aspects of which will return in subsequent chapters: social predation, emissions, habitat loss and fragmentation and biotic exchange. Sections 2.2-2.5 elaborate on each category and their proximal ecological effects according to the literature. Each of these sources of social impacts can cause loss of species. The extent of human activities and social impact is such that the survival of many naturally-occurring species is threatened. Currently 16,119 species are considered threatened (2006 IUCN Red List). The implications of biodiversity loss for ecosystems are discussed in Section 2.6.

Section 2.7 considers the evolutionary consequences of social impact and of biodiversity loss. This is examined in the light of two opposites forming the basis for evolution, viz. speciation or the generation of new species, and extinction or loss of existing species. Section 2.7 offers a brief discussion on reciprocal consequences for social systems, and concludes the chapter.

2.2 Social predation

Humans 'prey' on various naturally occurring species, and hence the term 'social predation'. Biological definitions identify a predator as a species that rapidly kills and eats other animals (see Chapter 3 and Glossary). Social predation emphasises that targeted species are removed precipitately and completely from their natural environments. However social predation differs from conventional predation in that it may not always lead to death of the prey (e.g. the capture of aquarium fish), and includes non-animal species (e.g. logging). 'Prey' are species that are: a source of food (e.g. fish); a source of raw materials and/or energy (e.g. trees); a source of pleasure from their capture (e.g. trout); a threat to humans and their activities (e.g. *Anopheles* mosquitoes, foxes); and of ornamental (e.g. aquarium fish), medicinal (e.g. various plants and fungi), or have, in some other way, value to humans (e.g. individuals held in zoos and botanical gardens).

Humans appropriate more than a third of all terrestrial production (Vitousek *et al*. 1986). As a result, large portions of some types of ecosystems have been simplified and remnant target populations down-sized. Remaining fragments often lack herbivores or predators that once provided important top-down constraints (Tilman & Lehman 2001), or species that perform specific ecological functions. Various terms are applied to such species, such as 'keystone species' and 'ecosystem engineers' (see also Chapter 6). Andelman and Fagan (2000) define a selection of such terms. Substantial changes to ecosystems, such as equilibrium shifts can be effected with the loss of such species (see Box 2.2).

Box 2.2 Down-sizing, shorter food chains and trophic cascades from overharvesting of top predators in kelp communities

Kelp (*Macrocystis spp*) may be found over large areas from warm temperate to subpolar coastal waters. They provide complex habitat for a great diversity of fish and invertebrates. Atlantic cod and other predatory ground fish were once extremely abundant in kelp forests along the coast of New England (USA) and eastern Canada, but have now been fished to exhaustion. Large, often 1.5 to 2 metres in length, and abundant cod have been fished from this area for some 5,000 years without evidence of decline. Mechanised trawling replaced hook-and-line fishing in the 1920's, resulting in a precipitous decline in abundance and size, and the eventual elimination of cod from coastal habitats in the 1980's. The average size of the few fish now caught is less than 40 cm (Jackson 2001).

Kelp is an example of an ecosystem engineer; its loss has had severe consequences for associated species. In the northeast Pacific, alternate stable states exist between kelp forests sustained by sea otters (*Enhydra lutris*), and barren grounds dominated by sea urchins (*Strongylocentrotus spp.* – Tegner & Dayton 1999). Sea otters eat sea urchins, and sea urchins eat kelp and algae. When hunting drove the sea otter population to local extinction, the release from predation allowed sea urchin populations to grow and resulted in their extirpation of the kelp forests. In turn, this led to less productive shorelines in terms of harvestable products. It also removed an important physical buffer, leading to an increase in coastal erosion. Re-established sea otter populations appear to have reversed this effect (Norberg 1999).

The strong effect of sea otters on the sea urchin, and in turn on the kelp, is evidence for a trophic cascade. A trophic cascade may be defined as a strong effect imposed by top predators such that it affects, not only the prey population, but also the organisms on which the prey feed, and so on down the food web (Pace *et al*. 1999; {Polis *et al*. 2000; Schmitz *et al*. 2000).

Social predation tends to be disproportionately directed towards large species due to their high value per unit mass (Western 2001; Novacek & Cleland 2001). The primary ecological effect is an increased risk of extinction from overharvesting. Freshwater and marine ecosystems have been the main targets of overharvesting; humans have become top predators in many marine food chains (Novacek & Cleland 2001). A tendency for targeted species, mainly large fish, to be replaced by other organisms, such as jellyfish or fish species of lower commercial value, has been observed. This replacement can lead to a new equilibrium and makes it questionable whether the stocks of the original species will ever recover (Jackson 2001). The ecological effects of heavy predation on large-bodied species include (Western 2001; Woodruff 2001; Tilman & Lehman 2001):

- down-sizing whereby the mean body size of species in communities will diminish;
- shorter food chains with increased risk of equilibrium shifts as a result of trophic cascades;
- further decreases in species richness and habitat patchiness because large-bodied predators and herbivores tend to be either keystone species or ecosystem engineers;
- shorter population cycle times and overall community turnover rates, more rapid rates of nutrient flow;
- increased capacity to recovery from change but decreased capacity to resist change (see also the discussion of resilience in Chapter 2);
- increasing influence of external agencies and stochastic events on community dynamics as the interaction networks and internal feedback linkages dominated by large animals weaken; and,
- loss of overall productivity with the loss of important functional groups.

The ecological effects of social predation may be delayed over time, and their importance underestimated in the presence of other social impacts. The large-scale mortality of Caribbean corals in the 1980's, as a result of overgrowth by macroalgae, provides an example. Current evidence suggests that this overgrowth was not linked to nutrient enrichment, but to social predation (Jackson 2001). Overfishing of large herbivorous species during the 19th century reduced their populations until only the sea urchin (*Diadema antillarum*) remained. Coral communities and macroalgal populations did not change noticeably until an epidemic decimated urchin populations. The time lag probably indicates ecological redundancy – multiple species available to fill a functional role.

Human activities can also promote predation by other species as a result of introducing them into new environments. This is a side effect of biotic exchange, discussed more fully in Section 2.5. Invasive species have various effects on ecosystems, but their predation on existing species is the most severe (Mooney & Cleland 2001). Examples may be drawn from pre-historical (e.g. extinction of land birds throughout Oceania with the introduction of rats and dogs – Grayson 2001), through historical (e.g. impacts of cats on tuatara populations in New Zealand – Towns *et al*. 2001), to modern times (e.g. cichlids and the Nile perch in Lake Victoria – Witte *et al.* 1992).

2.3 Emissions

Natural systems cater for the processing of the wastes from all organisms. This rarely causes problems, except perhaps locally or temporarily. The large size of human populations and of populations of their domesticated species, the density of settlements, the in-

creasingly large variety and volumes of wastes, as well as the release of substances into the environment for a purpose (e.g. fertilizers and pesticides) have led to an overloading of processing capability. The accumulation of substances with potentially negative effects on environmental media – soil, water and air – is termed pollution. The immediate vicinity of emission is often heavily impacted. Environmental transport mechanisms such as winds and rivers may increase the area of impact (e.g. acid rain) or concentrate substances in environmental sinks (e.g. harbour sediments) and so create spatial and temporal displacement between emission and impact. Emissions may also interact with each other. For example, enhanced rates for mercury methylation are linked to low pH, low salinity, the presence of decomposable organic matter (e.g. sewage or other organic pollution) and reducing environments. It is not possible to consider each of these parameters separately as they often interact, forming a complex system of synergistic and antagonistic effects (Ullrich *et al*. 2001; Haitzer *et al*. 2002).

Pollution affects the occupants and users of contaminated media. These effects, on humans as well as on naturally occurring species, have been of particular concern since the early 1960's. While much has been and is being done to abate emissions, new substances and new effects (e.g. endocrine disruption – see Legler 2001) are still being discovered. Recovery from pollution-induced environmental changes still faces severe problems with regards to both analysis and action (Novacek & Cleland 2001).

The ecological effects of pollution include the loss of sensitive populations, shifts in species composition, changes in the rates of biogeochemical cycling, bioaccumulation, and equilibrium shifts. They are often difficult to disentangle from other impacts. For example, eutrophication of Chesapeake Bay on the east coast of the USA can also be attributed to the loss of oysters and their filtration capacity, the loss of seagrasses with their support of sediment stability and their benthic oxygen production, as well as increased nutrients in runoff. These different factors have acted synergistically to increase phytoplankton at the expense of benthic resources and habitat (Jackson 2001). Emissions are also leading to effects at the global scale. Two examples are discussed and were chosen because of the attention they receive with regards to their potential effects on evolution.

2.3.1 Disruption of the nitrogen cycle

The scale and magnitude of human transformations of the physical environment are now so large that they are inducing global disruption of biogeochemical cycles. Virtually all of the substances limiting the growth, particularly of plants, are being affected (Novacek & Cleland 2001; Vitousek *et al*. 1997b). Nitrogen is unique among these in that its cycle includes a vast atmospheric reservoir that is not available to most organisms. Atmospheric nitrogen must be fixed (converted from inorganic to organic forms) before it enters food chains. The species composition and the diversity, dynamics, and functioning of many terrestrial, freshwater, and marine ecosystems are controlled, at least in part, by the supply of nitrogen. Many of the original plant species living in these ecosystems are adapted to low levels of available nitrogen, and function optimally in such environments (Tilman & Lehman 2001). Agricultural practices, combustion of fossil fuels, and other human activities have altered the global cycle of nitrogen substantially, increasing its availability over much of the Earth.

Disruption of the nitrogen cycle has led to increased nitrogen deposition on terrestrial ecosystems and increased nitrogen fluxes to lakes and oceans. Nitrogen deposition can be expected to have the greatest impact on ecosystems that are the most nitrogen-limited. Box 2.3 illustrates how nitrogen deposition could lead to local extinction, dominance by a few 'weedy' species, and communities susceptible to invasion. Nitrogen fluxes to aquatic ecosystems lead to eutrophication with increased abundance and dominance of ecosystem processes by microbes (Jackson 2001; Woodruff 2001) with subsequent loss of biological diversity (Micheli 1999) and diminished resistance of aquatic communities to invasive species (Stachowicz 1999).

Vitousek (1997b) reviewed available scientific evidence and concluded that human alterations of the nitrogen cycle have:

- approximately doubled the rate of nitrogen input into the terrestrial nitrogen cycle;
- increased concentrations of the greenhouse gas N_2O and of other nitrogen oxides that drive the formation of photochemical smog;
- caused losses of other soil nutrients, such as calcium and potassium (nitrate is readily leached from soils and may carry other cations with it);
- contributed to the acidification of soils, streams, and lakes in several regions;
- greatly increased the transfer of nitrogen to coastal zones (Mackenzie *et al*. 2002), with subsequent changes to the structure and function of coastal ecosystems; and
- accelerated loss of plant diversity, especially of those species adapted for efficient use of nitrogen, and subsequently of dependent animals and microorganisms.

2.3.2 Climate change and global warming

Life on Earth is based on carbon, the primary source of which is carbon dioxide in the atmosphere fixed by photosynthesis. Human activities, such as burning fossil fuels and converting natural ecosystems to agricultural and other low-biomass ecosystems, return carbon to the atmosphere as carbon dioxide. Carbon dioxide concentrations in the atmosphere have increased by nearly 30 percent since the beginning of the Industrial Revolution and will continue to increase for the foreseeable future (Vitousek *et al*. 1997b). The accumulation in the atmosphere of carbon dioxide, as well as nitrous oxide, methane and other greenhouse gases, may lead to global climate change via the Greenhouse Effect. Climate change is expected to cause the most warming at high latitudes (arctic and boreal zones), the least in the tropics, with intermediate changes elsewhere (Kattenberg *et al*. 1996).

The rate of warming is expected to be unusually fast, but not without precedent (Roy *et al*. 1996; Houghton *et al*. 1996). However most living species have had little experience with global temperatures as warm as today's (Webb & Bartlein 1992). The growth rates of plants are temperature-dependent, with species (and genotypes) having optimal growth and competitive ability at particular temperatures and thus in particular climates. The geographic ranges and abundances of many terrestrial plants are limited by temperature extremes. These factors are one source of the geographic separation of species along continental climatic gradients, with different plant species specialised on different portions of the growing season (Tilman & Lehman 2001). The ability of species to respond to future climatic oscillations by shifting their ranges will be greatly reduced by habitat fragmentation, discussed in the next section (Woodruff 2001).

Box 2.3 Expected response of plant communities in a low nitrogen (N) habitat to greatly elevated nitrogen deposition (Tilman & Lehman 2001)

Plants species can be represented by the proportion of biomass in roots, stems and seeds. In low nutrient habitats superior competitors have high root biomass, low stem and seed biomass and moderate leaf biomass. Such superior competitors co-exist with progressively poorer competitors that are better dispersers (so-called 'weedy' species). Figure A provides a plot of stem, root and seed biomasses for plants in such a habitat. The enclosed area represents the 'trait space' for this habitat. (Note that the proportion of leaf biomass is not shown in these diagrams and accounts for the remaining proportion of biomass.)

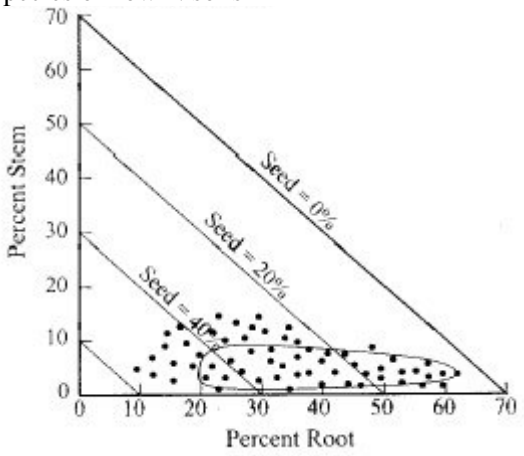
In a fertile habitat, competition for light results in a superior competitor's being taller and having a greater stem biomass. As with nutrient poor habitats, these superior competitors co-exist with poorer competitors that are better dispersers. See Figure B. If the nutrient-poor region in Figure A experienced rapid and high rates of nutrient deposition, only two of its original species would fall within the new trait space, as shown in Figure C, with two effects.

Firstly, both of the original species are weedy species. Under conditions of elevated N, they can be expected to increase in abundance where present, and to spread rapidly to suitable sites. The vast majority of the original species would be competitively displaced by the new dominants.

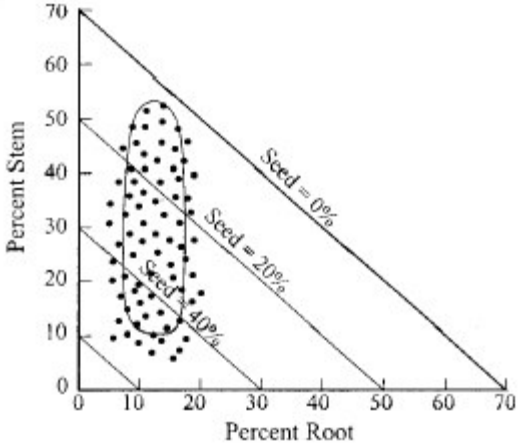
Secondly, the new trait space is almost empty. Species with appropriate traits should be able to invade the region.

This analysis suggests that elevated nitrogen deposition can lead to: local extinction; dominance by the few species that were formerly rare; and, an ecosystem highly susceptible to invasion and species turnover until a community such as that of Figure B has developed.

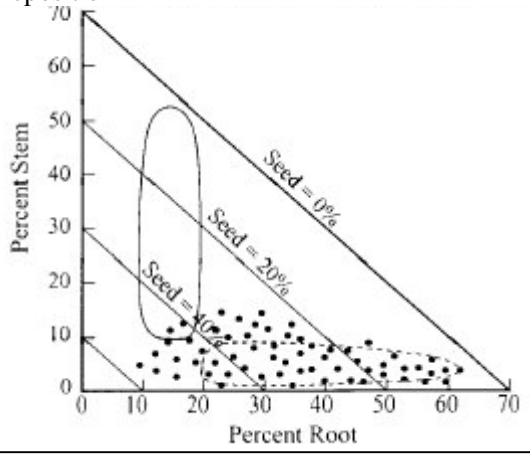
A. Species on low N soils



B. Species on high N soils



C. Empty Niches because of high rates of N Deposition



The ecological effects of climate change are reviewed and summarised by Gitay *et al*. (2001) and, for marine ecosystems, by McLean *et al*. (2001). Ecosystem responses to climate change include: changes in the distribution of species; changes in ecosystem boundaries and biomes; changes in phenology, the timing of biotic and abiotic processes

and events; changes in the structure of communities; changes in water flow and level leading to impacts on aquatic habitats, waterfowl, and riparian forests; polewards movement of biota; and, increase in frequency and/or intensity of disturbances caused by extreme climatic events. These responses also hold for marine ecosystems. Coral reefs have received much attention. Box 2.4 summarises some of the issues for corals.

Box 2.4 Climate change and corals

Corals reefs form as the result of an intimate nutritional symbiosis and mutualism between the coral animal and single-celled dinoflagellates known as zooxanthellae. Corals provide excretion products to their algal guests, and the algae provide photosynthetic products to their coral hosts. This obligate mutualism is probably responsible for the characteristically high rates of calcification of reef-building corals (Knowlton 2001). The ecological balance between these partners is potentially very sensitive to environmental conditions. It is unclear whether coral reefs will succumb to climate change. Adverse impacts stem from at least three sources.

Firstly, increased atmospheric CO_2 and uptake by oceans is predicted to cause an increase in the acidity of surface seawaters (IPCC 2001). This could adversely affect biocalcification by corals and other coralline species (Kleypas *et al*. 1999).

Secondly, sea level rise may be greater than the capacity of reefs to grow vertically. Healthy coral reefs, with an upper growth limit of 10 mm/year will probably be able to keep up with projected rates of sea-level rise (Buddemeier & Smith 1988; Schlager 1999). Concern lies with the fact that over half of the world's coral reefs are estimated to have been degraded (Wilkinson 2000; McCarthy *et al*. 2001).

Thirdly, higher temperatures cause coral bleaching, the result of expulsion or death of zooxanthellae. Bleached corals can survive for weeks or months, but their growth and reproductive output are reduced and eventually they die. Temperatures as little as 1ºC over the normal seasonal maximum can cause substantial bleaching, as evidenced by bleaching on a worldwide scale in 1998 with its unusually strong El Niño-Southern Oscillation event. However, coral-algal mutualisms have some capacity to withstand stress. Different zooxanthellae exhibit different susceptibility to bleaching and ability to recolonise bleached hosts. Reefs may be able to survive increases in sea temperature by shifts in the kinds of zooxanthellae that corals host. The long-term consequences of such shifts are unknown. Symbionts that colonise bleached corals are probably rapidly growing, opportunistic or stress-resistant and may not be ideal partners from the coral's perspective (Knowlton 2001).

Marine and coastal ecosystems face two additional sources of concern with global warming (McLean *et al*. 2001). The first is the impact of sea level rise and increased storm frequency on coasts. The second relates to oceanic circulation patterns. Rahmstorf (1999) and Wood *et al*. (1999) discuss the possibility of disruption of Atlantic circulation patterns, in particular the North Atlantic thermohaline circulation that warms Western Europe. Similar concerns exist for the convergence of warm and cold waters responsible for the nutrient-rich upwelling off the coast of Antarctica where changes could reduce krill production (Myers 1997). The frequency or intensity of the El Niño-Southern Oscillation may change as a result of global warming (Timmerman *et al*. 1999).

Walther *et al*. (2002) reviewed ecological responses to recent (last 30 years) climate change. The authors argue that there is a coherent and visible pattern of change reflected in organisms' phenology, their composition and dynamics, and the range and distribution of species. It is generally agreed that climatic regimes influence species' distributions, and that with general warming trends, these 'climate envelopes' will be shifted towards

the poles or higher altitudes. Walther *et al*. identify latitudinal and altitudinal range shifts for a number of species. They conclude that it is clear that communities are already undergoing re-assembly attributable to climate change, but that the inherent asymmetry in change processes complicates predictions of ecological response.

Finally, Root *et al*. (2003) and Parmesan and Yohe (2003) report on analyses that reveal a consistent temperature-related shift in species that match climate change predictions. The balance of evidence from these studies strongly suggests that a significant impact of global warming is already discernible in animal and plant populations. Parmesan and Yohe documented range shifts averaging 6.1 km per decade towards the poles and significant mean advancement of spring events by 2.3 days per decade.

2.4 Habitat loss and fragmentation

Habitat loss occurs when natural ecosystems are converted for human use by, for example, agricultural, urban and industrial development, transport and communication networks, ports and harbours, etc. Conversion inevitably leaves remnant habitats and ecosystems that become 'islands' in a sea of human activity. The term fragmentation refers to this fracturing of habitats and the severing of spatial connections among populations and communities. Habitat loss and fragmentation reduce the amount of habitat available for occupation and dislocate spatial links within populations and communities. The current scale of habitat loss and fragmentation is such that it threatens many species with extinction (Templeton *et al*. 2001; Western 2001; Beissinger 2000; Owens & Benneth 2000). Forecasted needs for the human population over the next few decades will, if anything, accelerate demands on natural habitats, and so both loss and fragmentation can be expected to increase (Tilman & Lehman 2001; Novacek & Cleland 2001).

The primary ecological effect of habitat loss is local species extinction. Habitat fragmentation isolates remnant populations and communities, converting sympatric to allopatric populations. This could lead to new species through founder effects – different selective pressures in different populations – or as a result of genetic drift (Schluter 2001). However, speciation is dependent on the continued viability of population islands. Decline in species abundance, distribution and interspecific interaction as a result of fragmentation tends to produce smaller populations (Tilman *et al*. 1994; Gonzalez *et al*. 1998) that are less viable because of increased vulnerability to stochastic processes such as floods, fire, epidemics, and to edge effects (Soule 1987). Edge effects are a direct product of the increase in habitat edge as a result of fragmentation. Some species benefit from ecotones, but mounting evidence reveals that abrupt edges negatively affect many species and ecological processes. Edge effects are remarkably diverse and include: microclimatic changes; increased predation due to an influx of generalist predators from surrounding modified habitats; altered patterns of pollination, seed dispersal, nutrient cycling and carbon storage (Laurance 2000). Edge effects also create ecological traps, which may exacerbate population declines from other sources (Schlaepfer *et al*. 2002).

Species in fragmented environments may eventually succumb to secondary extinction or 'extinction debt' (Tilman *et al*. 1994). These authors emphasise the roles of low population densities and/or poor dispersal abilities in secondary extinction, even if species are competitively superior (Tilman *et al*. 1994; Western 2001). In part, secondary extinction

is caused by the genetic erosion of populations, the loss of genetic diversity in populations subjected to anthropogenic stress (Straalen & Timmermans 2002). Habitat loss and fragmentation reduce population sizes and alter the balance between gene flow and genetic drift, thereby facilitating strong directional selection, inbreeding and genetic homogenisation in local populations (Straalen & Timmermans 2002; Templeton *et al*. 2001). Such genetically homogenised populations will be more likely to experience high infection rates and rapid spread of pathogens. They are less likely to have sufficient variability to respond to environmental change through the process of adaptation. Without sufficient gene flow, effective adaptations will be unable to spread throughout the species from their local population of origin.

The conversion of natural habitats to human land use not only homogenizes genotypes, it also homogenises landscapes. Human landscapes display convergent ecosystem properties in species assemblages, soil characteristics, and biogeochemical cycles. Human land use has a dampening effect on stochastic events and disturbance as these threaten the security of human activities. Loss of disturbance is another route to ecosystem simplification and homogenisation (Western 2001).

The species-area relationship (SAR) can be used to assess the rate at which species are lost with habitat loss. The SAR is one of the cornerstones of biogeography (May 1975; Rosenzweig 1995), and formulates the relationship between the increase in number of species S as the area A of a habitat increases. The relationship is given by:

$$S = cA^z \qquad \text{Eq. 2.1}$$

Much effort with the SAR has focused on determining values for z, and so the extent of non-linearity in the curve (see Figure 2.2). A small value of z means that the number of species increases slowly with area. The species-area relationship has also been used to predict species loss as a result of area loss (e.g. Pimm & Askins 1995; Pimm *et al*. 1995, Brooks *et al*. 1997, and Pimm 1998 in Ney-Nifle & Mangel 2000). See also Figure 2.2(b). In his review of the effects of habitat fragmentation on birds and mammals, Andrén (1994) argued that the decline in population size of a species living in the original habitat was linearly related to the proportion of original habitat lost; that $z = 1$. Such a value for z with species loss following habitat loss is also supported by Rosenzweig (1995 – see also Rosenzweig 2001).

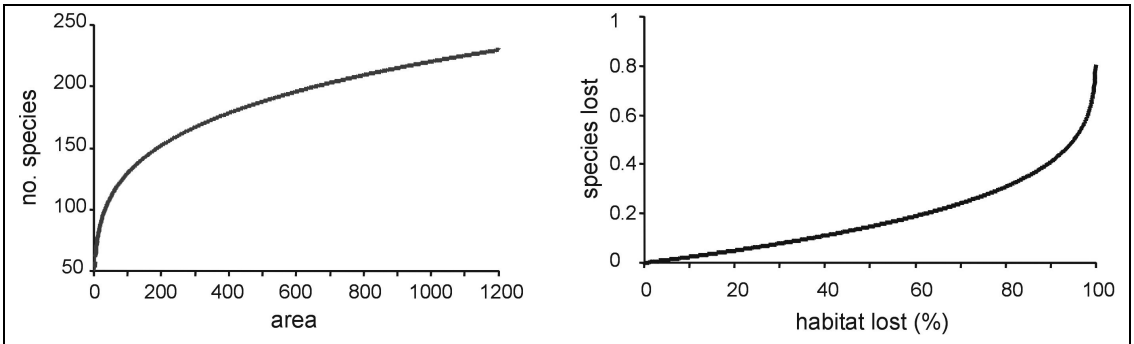


Figure 2.2 The species-area relationship predicts (a) the non-linear increase in species as area increases, but can also be used to predict (b) the loss of species as habitat declines (Ney-Nifle & Mangel 2000; z = *0.23)*

There are two points of concern in the application of the species-area relationship. The first is that both the intercept *c* and the exponential *z* tend to be treated as constants yet both may change as area changes (various references cited by Rosenzweig 1995). The second is that there may be alternative equilibria in species numbers at intermediate habitat sizes (Ward & Thornton 1998). A very real possibility exists of a non-linear and discontinuous relationship between habitat fragmentation and biodiversity (Metzger & Décamps 1997; Muradian 2001).

2.5 Biotic exchange and invasive species

The composition of biotic communities is undergoing dramatic change. The kinds of communities existing now are quite different from those that have existed in recent geological times (Mooney & Cleland 2001). One of the drivers of this change is human-mediated introduction of species (biotic exchange) to new areas (Novacek & Cleland 2001; Tilman & Lehman 2001; Mooney & Cleland 2001). Coastal marine habitats are among the most heavily invaded, in part due to the transport of species by ships (Cohen & Carlton 1998; Grosholz 2002). Biotic exchange increases species richness, but it also promotes homogenisation of biotas and can adversely affect native species populations (Mooney & Cleland 2001). Its effects on oceanic islands and endemic biological diversity have long been recognized (Vitousek *et al*. 1997b). Biotic exchange represents a human-caused breakdown of the regional distinctiveness of Earth's flora and fauna.

The numbers of individuals and species being transported across biogeographical barriers every day is presumably enormous, but only a small fraction of these species ever become established, and of these generally only about 1% become invasive (Williamson 1996 in Mooney & Cleland 2001). An invasive species is an introduced species that comes to degrade human health and wealth, to alter the structure and functioning of otherwise undisturbed ecosystems, and/or to threaten native biological diversity (Vitousek *et al*. 1997b; Lee 2002). The factors that control establishment and invasion are not well understood (Mooney & Cleland 2001). Physiological tolerance, the normal increase in size and distribution of a population, biotic and/or abiotic environmental change after establishment, as well as phenotypic plasticity allowing rapid adaptation would appear to be involved (Crooks & Soule 1999 in Mooney & Cleland 2001; Lee 2002).

There is disagreement among ecologists as to the magnitude of impact caused by invasions. Such disagreement is partly due to constraints in good baseline data on the distribution and abundance of original species assemblages as well as a limited ability to distinguish invaders with minor from those with large effects (Parker *et al*. 1999). Even so, the economic costs associated with the more publicised exotic invaders, such as agricultural pests, zebra mussels and plant pathogens, total approximately US$137 billion per year in the USA alone (Pimentel *et al*. 2000). Additions to endemic communities have become substantial (see Table 2.1). There are few geographic generalities to these trends, although islands appear to have borne the brunt (Mooney & Cleland 2001).

Table 2. 1 Percentage of introduced plant species in select countries (Heywood 1989)

Country/Region	Native Species	Introduced Species	Percent Introduced
Antigua/Barbuda	900	180	10
Australia	15,000-20,000	1,500-2,000	10
Austria	3,000	300	10
Canada	3,160	881	28
Ecuador (Rio Palenque)	1,100	175	15
Finland	1,250	120	10
France	4,400	500	11
Guadeloupe	1,668	149	9
Hawaii	1,200-1,300	228	17.5-19
Java	4,598	313	7
New Zealand	1,790	1,570	47
Spain	4,900	750	15

Introduced and invasive species can adversely affect the abundance of native species through, for example, predation, competitive suppression, changes in disease incidence and changes in the physical habitat such as fire frequency or nutrient cycling (Tilman & Lehman 2001). As the volume of global trade increases, so will the rate of establishment of introduced species (Mooney & Cleland 2001). Further, immigration increases the population sizes of these species and so builds-up their invasive potential. The future ecology of most areas is likely to display the effects of invasive species.

2.6 Biodiversity loss

2.6.1 Introduction

The sources and proximal ecological effects of social impact, as are currently understood, have been outlined above. However generalisation of the consequences of social impact is constrained by our limited ability to 'up-scale' effects on species or at local spatial scales to consequences for ecosystems and global processes. Perhaps as a result of this inability, the hallmark of social impact has become the loss of species and of biological diversity. The evidence for reduced species diversity, as an ecological consequence of social impact, is not conclusive but largely accepted, as indicated by the Convention on Biological Diversity. The Millenium Ecosystem Assessment (2003) estimated that 10-30% of mammal, bird and amphibian species are under threat of extinction due to human activities. The role of biodiversity in maintaining specific ecosystem functions was one of 100 ecological question of high policy relevance recently identified in the UK (Sutherland *et al*. 2006). The implications of biodiversity loss for ecosystems are still being hotly debated (e.g. Kaiser 2000; Cameron 2002). At the heart of the debate is the notion that species loss will bring ecosystems closer to collapse. This section introduces select stability concepts and summarises the diversity-stability debate.

2.6.2 Stability concepts

Stability is akin to constancy, while instability is akin to variability. Stability is addressed by a number of disciplines spanning the natural (e.g. physics, chemistry and ecology) and social sciences (e.g. economics). Traditionally stability has been couched

in terms of linearised dynamics seen as small departures from a stable equilibrium dominated by negative feedbacks that return the system to equilibrium after perturbation.

Theories based on the notion of stable equilibria have come under scrutiny. The study of complex systems has led to views on stability that expand to include non-linear and non-equilibrium dynamics as well as multiple stable states. There is also inconsistency between field and experimental research. Populations in the field and in the laboratory seem more likely to display variability than stability (McCann 2000). McCann highlights a discontinuity between stability experiments and equilibrium-based theory. He also argues that this discontinuity makes it difficult to unite theory and experiment in the diversity-stability debate currently raging among ecologists.

McCann outlines a viable ecological perspective on stability as an alternative to equilibrium population dynamics and argues that there is no a priori justification for the assumptions of equilibrium population dynamics that underpins much ecological theory. Real populations are variable. The persistence of complex communities may depend, to some degree, on population fluxes. Background population variability can provide species with the opportunity to respond differentially to their environment. One advantage of these differential responses could be to weaken the destructive potential of competitive exclusion. Ecology now has two definitions of stability (see Table 2.2), one based on equilibrium, and one that allows both equilibrium and non-equilibrium dynamics.

Table 2.2 Definitions of stability and related concepts (after Table 1 in McCann 2000)

Term	Definition
Equilibrium stability	A discrete measure that considers a system stable if it returns to its equilibrium after a small perturbation away from the equilibrium. A stable system, therefore, has no variability in the absence of perturbations.
General stability	A measure which assumes that stability increases as the lower limit of population density moves further away from zero. Under non-equilibrium dynamics, such limits to population dynamics generally imply a decrease in population variance.
Variability	The variance in population densities over time, usually measured as the coefficient of variation. Common in experimental tests of stability.
Equilibrium resilience	A measure of stability that assumes system stability increases as time required to return to equilibrium decreases after a perturbation. A rapid response means that a system recoils rapidly back to its equilibrium state.
General resilience	A measure of stability that assumes system stability increases as return time to the equilibrium-non-equilibrium solution decreases after a perturbation. A rapid response means that a system recoils rapidly back to its equilibrium-non-equilibrium state.
Resistance	A measure of the degree to which a variable changes after a perturbation. Frequently used as a discrete measure that assesses a community's ability to resist invasion (that is, if an invader fails, the community resists invasion).
Robustness	The ability of networks to resist fragmentation and secondary loss of network components (e.g. Dunne et al. 2002b).
Fragility	The converse of robustness. Fragile networks are prone to fragmentation and secondary loss of network components (e.g. Dunne et al. 2002b)..
Vulnerability	The converse of resilience. Mainly used in climate change studies where it is defined as the degree to which a system is susceptible to, or unable to cope with, adverse effects of climate change (Burton *et al*. 2002).

The definition of general stability implies decreased variability as a result of greater limits on density. This definition is closely related to field measurements of stability that tend to rely on variability in population or community densities. The discrepancy between theory and field would seem to be partially bridged with this alternative approach. As also shown in Table 2.2, stability definitions in ecology also include those based on a system's ability to defy change. McCann argues that it is possible to extend the notion of equilibrium resilience to a less restrictive form by defining resilience purely in terms of the return time after perturbation to an equilibrium or non-equilibrium attractor.

There are a number of additional terms in the literature that bear on stability. Three such terms, robustness, fragility, and vulnerability appear in Table 2.2. Robustness as a stability concept is the subject of further elaboration in later chapters.

The definitions of resilience and resistance in Table 2.2 are based on Pimm (1984). Ecology has produced another definition of resilience, coined in terms of the magnitude of stress from which the system can recover or the system's specific thresholds for absorbing various stresses (Holling 1973; Holling 1986). This definition closely resembles Pimm's resistance, but Holling and associates justify their definition by echoing some of the arguments of McCann for distinguishing between equilibrium and general stability, but adds the notion of multiple stable states. This perspective on resilience is relevant for the discussion of the adaptive cycle in Chapter 4, and so is briefly discussed.

Equilibrium resilience assumes that the behaviour of a system remains within the stable domain that contains this steady state (Holling 1996). Peterson *et al*. (1998) argue that such a single metric is insufficient for assessing the stability of ecosystems that can shift from one stability domain to another (see Scheffer *et al*. 2001 for a review). Holling's interpretation of resilience, 'ecological resilience', is intended to be a measure of the amount of change or disruption that is required to transform a system from one set of mutually reinforcing processes and structures to a different set of processes and structures. Peterson *et al*. illustrate the difference between these two interpretations by depicting an ecological 'state' as the position of a ball on a landscape (see Figure 2.3).

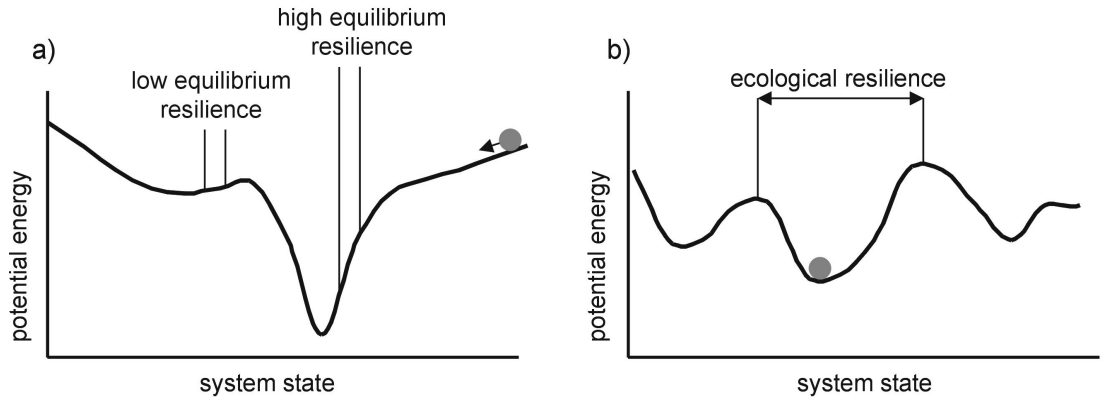


Figure 2.3 Difference between equilibrium (or engineering) resilience and ecological resilience (redrawn from Peterson et al. *1998)*

Gravity pulls the ball downward, so pits in the landscape are stable states. The deeper the pit, the more stable it is because increasingly strong disturbances are required to move the ball from the bottom of the pit. The steepness of the sides of a stability pit corre-

sponds to the strength of negative feedback processes maintaining an ecosystem near its stable state, and consequently engineering resilience increases with the slope of the sides of a pit (Figure 2.3a). Ecological resilience (Figure 2.3b) assumes that an ecosystem can exist in alternative self-organized or 'stable' states. It measures the change required to move the ecosystem from being organised around one set of mutually reinforcing structures and processes to another. The ecological resilience of a state corresponds to the width of its stability pit.

While measures for both types of resilience are of use to managers, Holling (1996) and Peterson *et al.* (1998) argue that equilibrium resilience, concentrating on conditions near a steady state, focuses on too small a portion of a system's stability landscape. It does not help to assess the response of a system to large perturbation, or whether gradual changes may cause the system to move from one stability domain to another. An example of the latter is phosphorus loading of freshwater bodies, and their 'flip' from being macrophyte-dominated with clear water to being phytoplankton-dominated with turbid water (Kay *et al.* 1999; Scheffer *et al.* 2001). Ecological resilience focuses on transitions between alternative states defined by sets of organising processes and structures. Holling and associates would argue that notions of stability and resilience need to encompass non-equilibrium dynamics and the possibility of multiple stable states, and to be coined in terms applicable to theoretical, experimental and field ecologists.

2.6.3 The diversity- stability debate

Early ecologists (e.g. Elton 1927; MacArthur 1955; Elton 1958) saw a direct relationship between the diversity or complexity of ecological communities, and their stability. They compared, for example, well-developed rainforests with simple agricultural systems. Rainforests are highly diverse systems with small fluctuations in population abundances and steady nutrient cycle; simple agricultural systems have few feedback mechanisms and are susceptible to stochastic events such as pest outbreaks and extreme weather conditions. The opposite idea, that diversity could lead to instability, was proposed by Robert May (May 1972; May 1973). May used mathematical models to represent dynamic equilibria of randomly interacting species. He showed that the larger the number of species or the higher the density of interactions, the less likely the system was to return to the equilibrium state after a small perturbation.

Ecologists have been very busy since May published his findings, attempting to specify the diversity-stability link. Natural systems are complex and diverse, so how can they exist and what makes them stable? Loss of biodiversity caused by social impact has added impetus and urgency to our understanding of this link. However, theoretical work has not resolved the role of various aspects of ecosystem complexity in stabilising ecosystems (e.g. McCann 2000), while experimental and comparative research (e.g. Tilman & Downing 1994; Naeem *et al.* 1994; Hooper & Vitousek 1997; Loreau *et al.* 2001) has yet to distinguish clearly the relative importance of changes in species richness versus loss or gain of particular species' functions in driving ecosystem functioning (Loreau *et al.* 2001; Huston *et al.* 2002). Progress is being made, and the main findings are summarised below. This summary draws heavily on Neutel (2001) and McCann (2000).

May's models assume random interactions among species, an assumption that clearly does not hold. Species eat, form partnerships, compete or may be dependent on other species for their habitat requirements. Feeding interactions tend to form a hierarchy, and it has been shown mathematically that the hierarchical structure of food webs contributes to community stability (DeAngelis 1975; Pimm 1982). Many aspects of food web structure have been related to stability, and theoretical studies have given some idea of which structures could be expected in natural systems. The emerging picture is not always clear-cut or consistent. For example, the role of omnivory was a destabilising factor in the models of Pimm and Lawton (1978), whereas Borrvall *et al*. (2000) reported that it reduced secondary extinctions in food webs subject to species loss, and Dunne *et al*. 2002b) showed that network robustness did not relate to omnivory.

May's models assume random interaction strength, and this assumption also does not hold. Ecologists have long recognised that there are strong and weak links in a community. Relatively little attention has been paid to interaction strength, partly because of a lack of agreement regarding its definition and treatment in theoretical models versus experimental studies (Paine 1988; Ruiter *et al*. 1995). It has been argued that the more species a consumer feeds on, the less strong will be the effect on each consumed species. While the greater number of interactions would be destabilising according to May's models, the lower average strength of the interactions could compensate for this (McCann *et al*. 1998). It has also been argued that consumers have a much stronger effect on the dynamics of consumed species than vice versa (Pimm & Lawton 1978). This has led to discussions on the relative importance of limitations by resource availability (bottom-up) and by predators (top-down) (Bonsall & Jones 1998). Cury *et al*. (2000) suggests that ecological control is exerted both up and down from intermediate trophic levels. Species in the middle ground may occupy a crucial position, e.g. anchovies, sardines and pilchards in oceanic food webs, or Cladocera in freshwater aquatic food webs.

Empirical studies have now made clear that most interactions in natural communities are very weak, spreading the direct effects of consumption and productivity throughout the web rather than focusing them at particular trophic levels (Paine 1988; Polis & Strong 1996). Both empirical and theoretical studies have indicated that the pattern of strong and weak interactions may be relevant for community stability (Yodzis 1981). Stability is enhanced when a few strong interactions are embedded in many weak ones (Paine 1988; Polis & Strong 1996; McCann *et al*. 1998), and by the simultaneous occurrence of strong 'top down' effects at lower trophic levels and strong 'bottom up' effects at higher trophic levels (Ruiter *et al*. 1995). McCann (2000) explains the underlying logic as follows. Weak interactions serve to limit energy flow in a potentially strong consumer–resource interaction, and therefore to inhibit runaway consumption that destabilizes the dynamics of food webs. Further, weak interactions mean weak consumptive influences on a resource when the resource is at low densities.

More recent research extends the diversity-stability analysis by considering trophic loops (Neutel 2001; Neutel *et al*. 2002). A trophic loop describes a pathway of interactions from a certain species through the food web back to the same species without visiting other species more than once. It is a closed chain of trophic links. Neutel and her co-authors developed a measure for 'loop weight' so that patterns of interaction strengths within a loop could be characterised. They found that weak and strong interactions were

distributed in such a way that the maximum weight of trophic loops was kept low, and certainly lower than a random distribution of interaction strengths would produce. In such random 'communities', strong interactions would not necessarily be coupled to weak interactions that mute their destabilizing potential. Diverse communities with random interactions and random strengths of interactions can then be expected to exhibit complex, oscillatory dynamics.

Neutel links three additional features of food webs to community stability. Firstly, detritus feedbacks, flows of dead matter to a detritus component at the bottom of the food web, give a large, positive, top-down effect, become stronger in more developed, complex ecosystems, and enhance their stability. Secondly, pyramids of biomass, commonly observed in food webs, enhance the stabilising distribution of weak and strong interactions. Thirdly, organisms higher in food webs generally have larger body sizes, longer life spans, as well as higher conversion efficiencies and so appear to lie behind the strong decrease in biomass over trophic levels.

A number of tentative conclusions have been reached. Some diversity is necessary to allow ecosystems to function while more diversity is necessary to ensure stability in a changing environment (Loreau *et al*. 2001). That more diversity is needed for stability than for function suggests that functional redundancy is crucial for stability. McCann (2000) concludes that recent advances indicate that diversity can be expected, on average, to give rise to ecosystem stability, but that diversity *per se* is not the driver of this relationship. It is less the number of species in a community, and more the nature and pattern of interactions among species and the properties of species that drive stability.

2.7 Evolutionary consequences of social impact

2.7.1 Introduction

The hallmark of social impact has become biodiversity loss, with species failing to adapt to changing conditions brought about by human activities. The above sections discussed current understanding of the ecological consequences of biodiversity loss. The evolutionary consequences are difficult to specify as evolutionary biology is not a predictive science. However consequences would appear to fall into two broad directions. The first treats the species lost and reflects concerns that humans are causing another extinction event. The second treats the species that survive, considers which species are most likely to be the progenitors of future species, and what future ecosystems might look like.

2.7.2 From biodiversity loss to mass extinction

The rate of biodiversity loss has raised fears that social impact is triggering another extinction event (e.g. Myers & Knoll 2001; Chapin *et al*. 2000). The long recovery times from past extinction events, observed in the fossil record, only adds to this concern (Erwin 2001; Kirchner & Weil 2000; Looy *et al*. 1999). A species becomes extinct if it is unable to evolve rapidly enough to meet changing circumstances, and/or if its niche disappears so that no capacity for rapid evolution could have saved it (Smith 1989). Mass extinctions are typically defined in terms of their irreversible impact on large numbers of species in diverse taxa across the globe and over a short period (Woodruff 2001). While

there is by no means consensus on whether or not current biodiversity loss constitutes mass extinction, current extinction rates are 50-500 times background rates and increasing (Woodruff 2001). Time lags in the ecological consequences of social impact, let alone the full effects of climate change, can only be expected to prolong or exacerbate these trends.

Solé (2000) argues that extinction has seldom been considered as a relevant ingredient in neo-Darwinian theories of evolution. The classical view of extinction involves a slow process of decline: species and groups of species gradually disappear, one after another, first from here, then from there, and finally from the world. The rapid, even massive extinction of entire groups was initially assumed to be due to incompleteness of the fossil record. This now seems not to be the case. Extinctions have occurred at different intensities in different moments of life's history. The fossil record shows many small extinction events, as well as a few, large-scale extinctions that wiped out a great part of Earth's diversity. Of particular note are the 'big five' mass extinction events that marked the ends of the Ordovician, Devonian, Permian, Triassic, and Cretaceous periods.

Two basic regimes appear to be involved in the overall pattern of extinction. The first is termed 'background' extinction and occurs primarily due to biological or ecological processes. The second is 'mass extinction' that is usually attributed to various sources of external stress such as climate change, tectonic activity and meteorite impacts. There is disagreement on the causes of mass extinctions, because of the presence of multiple causes and because similar events at other times have not led to mass extinction. For example, the currently acceptable explanation for the extinction of dinosaurs rests on a meteorite's impact. Solé (2000) points to the Montagnais impact (diameter of 45 km, about 51 million years ago) and an impact in the Kalahari Desert (diameter of some 350 km, around 144 million years ago), neither of which caused mass extinctions.

If we are in another mass extinction event, qualitative factors distinguish current extinctions from past extinction events (Novacek & Cleland 2001). Firstly, the cause of the present event is clear and intrinsic, arising from a single species – humans. Secondly, human activities give rise to considerable patchiness in extinction rates, with different habitats and regions suffering differently with regards to both the source and severity. Such patchiness in terms of cause and effect is not a feature of past extinctions. Finally, mass extinctions have been documented over long or imprecise timescales. The current extinction event is primarily a feature of the last 75-100 years.

The number of species extinctions in the history of life is almost the same as the number of originations (Raup 1993 in Solé 2000). Although mass extinctions probably account for the disappearance of less than 5% of extinct species, the evolutionary opportunities they have created have had a disproportionate effect on the history of life (Erwin 2001). However the evolutionary response to mass extinction is slow on human time scales, difficult to predict, and geographically heterogeneous (Jablonski 2001). Theoretical considerations and simulations suggest that the empty niches created by a mass extinction should refill rapidly after extinction ameliorates. However empirical studies reveal more complex dynamics. Far from refilling ecospace (the sum of all available niches), mass extinctions appear to cause its collapse. Ecospace must then be rebuilt during recovery, and this reconstruction could lie behind long recovery times (Erwin 2001).

Survivorship and extinction during extinction events is not random, but it often fails to coincide with patterns during 'normal' times with background extinctions. Mass extinction events also remove the successful incumbents of ecosystems, and not just the marginal players that normally would be at risk of extinction. This leads to differential survival that does not promote the long-term adaptation of the biota (Jablonski 2001). Parallels exist with current selective pressures exerted by social systems. These would appear to favour species capable of surviving in human-dominated landscapes, independent of their success in landscapes dominated by natural processes.

2.7.3 To boldly speciate?

Ideas on species and their formation have always been a key part of biology. Even so, there is no consensus on what exactly a species is. To illustrate, the dynamic nature of evolution means that a single species today might be two or more different species tomorrow; the point at which one becomes two is difficult to discern. Strictly speaking, speciation consists of evolution that magnifies differences among individuals so that interbreeding and recombination between populations is prevented (Barton 2001; see Schluter 2001 for a summary of different modes of speciation).

Social impact is redirecting speciation. By causing a widespread loss of species and populations, it is reducing the gene pool underlying phenotypic variability and from which phenotypes can be selected. It is promoting the mixing of biotas that under other conditions would remain distinct and it is selecting for species that can survive in human-dominated landscapes. Genetic loss combined with the genetic 'swamping' of rare species by common congeners suggest that future natural systems will be characterised by progressive depletion and homogenisation of biotas (Myers & Knoll 2001; Western 2001; Woodruff 2001). The associated decline in genetic and phenotypic variability is likely to disrupt or diminish the capacity for adaptation, and this will have implications for speciation (Templeton *et al*. 2001; Myers & Knoll 2001).

Habitat fragmentation plays a large role in these effects. Fragments are surrounded by human-dominated systems characterised by homogenisation while fragmentation augments genetic drift and diminishes gene flow. This can be expected to reduce genetic variation within local populations and prevent the spread of adaptive complexes outside their population of origin. In theory, it could also lead to new species through founder effects. However, Templeton *et al*. (2001) point out that founder events have played an important role only when ecological opportunities were expanding, not contracting as they are now. Rosenzweig (2001) argues that a decline in speciation rates will occur as a direct result of the decline in area available for natural systems. Speciation and area may be related due to two factors: firstly, species with larger geographical ranges speciate faster; and secondly, loss of area drives up extinction rates thus reducing the number of species available for speciation.

Depletion and homogenisation can be expected to change the rates of evolutionary processes differently in different groups (Woodruff 2001). The expansion and intensification of human-dominated landscapes will shrink and homogenise habitats, reduce population sizes, and fragment their range by imposing physical or biological barriers to dispersal (Western 2001; Myers & Knoll 2001). This will select against poor dispersers and

against large species that have large ranges. Many of the latter are already under threat from social predation. Large vertebrates can be expected to be severely affected, and their speciation is likely to end (Western 2001; Myers & Knoll 2001). However, ecological generalists, and in particular small, easily dispersed species able to tap into the production cycle of human-dominated landscapes, will be favoured by selection. Generalists are typically *r*-selected weedy species (see Table 2.3) and pathogenic and competitive microorganisms (Western 2001; Woodruff 2001). Greater abundance and increasing dominance by these 'weedy' taxa will lead to an outburst of speciation; they will become the progenitors of a series of new species that will become progressively better adapted to the new conditions (Tilman & Lehman 2001).

Table 2.3 Characteristics often associated with r- *and* K- *selection (Strickberger 1996)*

Character	*r*-selected	*K*-selected
Climate	variable or unpredictable	fairly constant or predictable
Resources and habitats	usually broad range	relatively narrow range
Causes of mortality	often catastrophic and density independent	mostly density dependent
Survivorship	very high mortality at younger stages with high survivorship at later stages	either constant at most stages, or low until certain stage is reached
Competitiveness	variable, mostly weak	usually strong
Length of life	relatively short, usually less than 1 year	longer, usually more than 1 year
Selection for:	rapid development	slower development
	rapid increase in numbers	greater competitive ability
	early reproduction	delayed reproduction
	small body size	large body size
	semelparity	iteroparity
	many small offspring	fewer and larger offspring
	increased productivity (=quantity)	increased efficiency (=quality)

Despite only a rudimentary understanding of how human actions are altering the evolutionary future, the evolutionary consequences of social impact suggest future ecologies characterised by: homogenisation of biotas and the proliferation of opportunistic species. The latter will lead to a pest-and-weed ecology and an outburst of speciation among taxa that prosper in human-dominated ecosystems.

2.8 Social response

It can be argued that human evolutionary success is proof of an ability to modify ecosystems to advantage and that social systems can and will take care of the environment in due course. This attitude is encompassed in the environmental Kuznet's U-curve or EKC (Selden & Song 1994), which postulates that environmental clean-up follows wealth creation. However, doubts have been raised as to whether the EKC-relationship holds. Western (2001) argues that the EKC does not apply to fisheries and forestry in the developed world, let alone in poorer nations. EKC has been shown not to hold for some air pollutants, such as carbon dioxide (Holtz-Eaken & Selden 1995 and Harbaugh *et al*.

2000 in Tisdell 2001) as well as carbon dioxide, nitrogen oxides and sulphur dioxide (Bruyn *et al*. 1998; Opschoor 1997). If environmental care is not a natural spin-off from wealth creation, the issue then becomes whether, and how, care for the environment can be stimulated, and how environmental damage can be decoupled from economic growth.

"The Future of Evolution" was the title of the colloquium, held at the National Academy of Sciences of the USA in March 2000, which provided some of the literature cited in this chapter. This colloquium also addressed aspects of the social response to the above evolutionary consequences. Two main directions for future environmental research and management were identified at a colloquium, "The Future of Evolution", held at the National Academy of Sciences in March 2000 and published in their Proceedings (volume 98, issue 10). The first was a more evolutionary perspective in environmental management, which would add even more weight to issues of intergenerational equity within the sustainable development debate. Few specifics were offered to illustrate such a perspective. The problem is that thirty years (i.e. one human generation) is considered 'long term' in environmental management while relatively short term with regards to evolution. Such a time dimension poses difficulties in social disciplines where uncertainty in human behaviour, consumer preferences and societal trends constrains much analysis to around a few years at most.

The second was explicit promotion and management of interactions between social and natural systems. Participants argued that conservation and restoration in human-dominated ecosystems must strengthen connections between human activities, such as agricultural or harvesting practices, and the ecosystems on which they depend. Promising approaches in this regard were identified, and included 'reconciliation ecology' and 'countryside biogeography'. Reconciliation ecology addresses how to modify and diversify anthropogenic habitats so that they would harbour a wide variety of species; reconciliation ecology could lead to the development of management techniques that allow humans to share their geographical range with wild species (Rosenzweig 2001). The goals of countryside biogeography include: determining what elements of biodiversity are best able to persist in altered habitats; establishing the relationship between intensification of land use and an area's conservation value; evaluating the importance of remnant habitat to the delivery of ecosystem services; and finding ways to enhance the delivery of environmental services from human-dominated landscapes (Ehrlich 2001). Ehrlich argues that this work could be extended to examine the possible impact of various patterns of habitat alteration on evolutionary trajectories and so to seek ways to enhance the evolutionary potential of communities persisting in areas heavily impacted by human activities.

Combined, these two research directions argue for a coevolutionary perspective in environmental management. The language of the colloquium is ecological, but it serves to complement similar arguments made by environmental and ecological economists (see Chapter 1). The notion of a longer time frame in management is not new, nor is the focus on interactions between natural and socials systems. What is new is a shift in environmental management strategy, with the notion of adaptation complementing the traditional focus on mitigation.

2.9 Conclusions

This chapter has taken a broad tour through the causes and effects of social impact on ecosystems. Four categories of social impact have been identified, distinguished by the type of interaction between the two systems. Each of these sources of social impacts generates its own set of ecological effects, including the number and types of species whose viability is threatened.

The hallmark of social impact has become biodiversity loss. Concerns regarding biodiversity loss revolve, ultimately, around the capacity of ecosystems to supply environmental goods and services, not only for current but also for future societal use. The fossil record, while incomplete, clearly shows the long recovery times associated with past mass extinction events when ecosystems apparently collapsed. It also shows the loss of species that would not normally be at risk of extinction. Species currently at small risk of extinction are frequently pest species, so designated because they cause a direct or indirect cost to social systems.

The future performance of ecosystems experiencing biodiversity loss is uncertain. The relationship between ecosystem stability and diversity is not clear-cut, but that one exists seems inevitable. Much research effort has been and is being expended to clarify the relationship. Our current knowledge suggests that it is not biodiversity per se that lends stability to ecosystems. One factor would appear to be the pattern of interactions among the ecological community.

The pattern of interaction and the species under threat from social impact are themes that will be developed further in this dissertation.

This chapter has also shown that the argument for a coevolutionary perspective in environmental management, while largely deriving from economists, is also reflected in ecological thinking. In my attempt towards developing specifics for such a perspective, I turn to very different sources of literature in the next two chapters. Chapter 3 takes a rigorously biological view of coevolution. The term, after all, derives from evolutionary biology, and species have a considerable history of coevolution. The ‘up-scaling’ of these lessons, from how species coevolve to how systems might coevolve, is fraught with difficulties. On the whole, evolutionary biologists would not accept this up-scaling, arguing that evolution at hierarchical levels above the individual could be reduced to processes operating at the level of the individual. The notion of coevolution between systems derives from the study of complex systems where system evolution is considered almost axiomatic. The progression from the evolution of species to the evolution of systems is made in Chapter 4. Chapter 4 also returns to recent research on complex networks, where the pattern of interactions among system components is emphasised.

3. Coevolution between Species

"It was Ponder's particular genius that he had …[considered] the phrase, 'How do you know it's not possible until you've tried?' And experiments … had found that, indeed, many things are not impossible until they have been tried."

"The Last Continent", Pratchett 1998, p23

3.1 Introduction

Evolution means change over time. In biology it refers to the descent of organisms with modification in form, physiology and/or behaviour over generations (Ridley 1996). Charles Darwin (1859) proposed natural selection as the mechanism behind evolution. Natural selection ensures that some kinds of individuals in a population contribute more offspring to the next generation than others. These individuals are, in general, better suited to their environment. They exhibit properties that enhance their ability to survive and reproduce. An explanation for natural selection came with work of Gregor Mendel (1866) on heredity, and was combined with Darwin's natural selection in the first decades of the 20th century to yield the synthetic theory of evolution, the basis for modern evolutionary biology. Natural selection is complemented by gene flow and genetic drift in creating evolution. Gene flow occurs because individuals move among populations; genetic drift occurs through random changes in allele frequency over time. The former decreases genetic variation within but increases it among populations; the latter increases variation within but decreases differentiation among populations.

Evolutionary biology attempts to understand biological diversity and organismal design. While predominantly retrospective, it is also capable of providing valuable lessons for the future. One area where evolutionary biology may contribute to future environmental management is related to extinction events, also discussed in Chapter 2. Evolutionary bi-

ology is also the study of conflicts, not only among competitors and between eaters and the eaten, but also between parents and offspring, brothers and sisters, and genes with different transmission patterns (Stearns & Hoekstra 2000). Participants in conflicts must make the best of a bad situation that they often cannot escape.

Organisms adapt in response to their environment, as a result of interacting with both biotic and abiotic components. The presence of other species, and particularly the specialised links and networks of interaction among species, have produced much of the diversity of life (Thompson 1994). Here evolutionary biology overlaps with ecology. Adaptation in response to interactions with other species sometimes results in reciprocal evolutionary change. Reciprocal evolutionary change is coevolution.

The notion that social and natural systems coevolve received considerable attention in the mid-1990's as a result of publications from two economists: Richard Norgaard (1994) and John Gowdy (1994). Social structures and their processes impinge on the environment, thus modifying and changing it. These changes shape the structure of social systems in turn, so that they are better positioned to adapt to the changing environment. Interaction between the two systems is constant and reciprocal. Coevolution, in this context, highlights the complex coupling of the two systems now and into the foreseeable future (Turner *et al*. 1999; Lorenzoni *et al*. 2000a).

This chapter reviews current knowledge of the evolutionary processes triggered by species interactions and resulting in adaptation by one or both species (see Figure 3.1). I draw lessons from this knowledge to assist environmental management, and analogies for the coevolution of social and natural systems. Specific objectives of this chapter are:

- to identify evolutionary processes, and the mechanisms behind them, which are triggered by species interactions;
- to consider which of these may be considered ‘desirable’ in the context of the coevolution of social and natural systems; and,
- to identify analogies that could apply to environmental management.

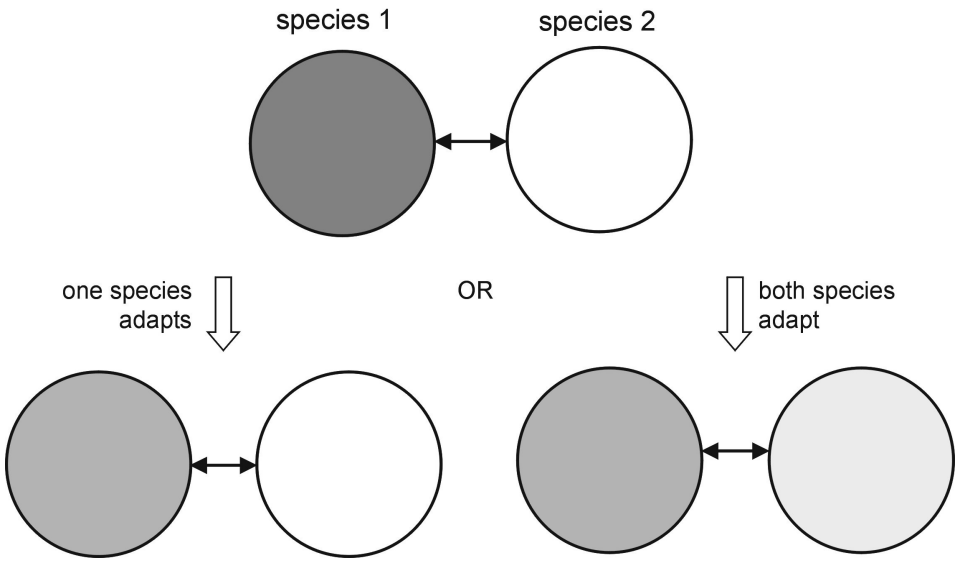


Figure 3.1 Species interactions leading to adaptation by one or both species

Desirability is defined anthropocentrically in terms of two criteria: long-term co-existence, and the potential for both social and natural systems to benefit from interaction. Such a definition draws from the debate around sustainable development (Barbier 1987), which relates to the perpetual availability of some basic set of ecosystem services for use by human societies (Farber 1991). For the purposes of this discussion, two criteria for desirability are identified: continued co-existence of participants, and potential for both participants to derive net benefits from the interaction

The chapter is structured as follows. Section 3.2 elaborates on coevolution, as studied by biologists. Interaction is a necessary prerequisite, and so this section also presents frameworks for characterising interactions. It identifies five evolutionary paths along which species may move as a result of interaction. Section 3.3 discusses each of these paths and their underlying mechanisms. The discussion in Section 3.3 focuses on evolution as it, inevitably, occurs over time. Section 3.4 considers coevolution across space. Section 3.5 draws lessons for environmental management particularly in the context of the interaction between social and natural systems. Section 3.6 concludes the chapter by considering how interspecies coevolution could be upscaled to coevolution between systems. Definitions of terms may be found in the glossary at the end of the dissertation.

3.2 Evolution and interaction

3.2.1 What is coevolution

Neo-Darwinism argues that evolution can be triggered by interactions among species and between species and their physical environment. Adaptation to another species, unlike adaptation to the physical environment, can produce reciprocal evolutionary responses. These reciprocal responses can: thwart adaptations by the other (e.g. Dawkins & Krebs 1979); remove the need for further adaptation (e.g. Schluter 2000); or lead to magnification (e.g. Hinckle *et al*. 1994). Reciprocal evolutionary change is coevolution. An easily recognisable example of coevolution is provided by flower shape and colour, and the mouthparts and sensory perception of insect pollinators (Barth 1991, Labandeira *et al*. 1994). The coevolution of flowers and pollinators has made a potent contribution to biological diversity: flowering plants are the largest present-day plant group with some 250,000 known species; pollinating insects such as bees, bee flies, flies, butterflies, moths and beetles comprise some 750,000 of the known 1.2 million animal species.

Coevolution was first defined in the 1960's (Ehrlich & Raven 1964) and the subject of much debate in the 1980's (Futuyma & Slatkin 1983). Was it 'specific' – one species with another – or 'diffuse' – a group of species with another group of species, as with flowering plants and their pollinators? Coevolution is now seen an umbrella term for a variety of processes and outcomes of reciprocal evolutionary change (Thompson 1994). The focus of attention now lies with how species interactions evolve in time and across space (Thompson 1999a; Thompson 1999b; Thompson 1999c).

Species interaction is a prerequisite for coevolution. However interaction does not always result in coevolution. Organisms are subject to multiple sources of selection. Consequently interaction between two species (or species groups) may lead to no adaptation, adaptation by only one, or adaptation by both. The difference between evolution by one

participant in an interaction and coevolution can be fine, particularly if the features of a species' biotic environment remain constant for long periods of time (Futuyma & Slatkin 1983). This chapter does not distinguish between evolution and coevolution so long as adaptation occurs as a result of interaction between species (*cf* interaction with an abiotic factor where adaptation cannot be reciprocated). The distinctive feature of coevolution is that the interaction itself is responsive to evolutionary change by participants. This is shown in Figure 3.1 as a change in the line indicating interaction between the species.

3.2.2 Interactions between species

Species interactions can result in a positive, negative or no effect on participants. Cross-comparison of these effects leads to the conventional matrix of outcomes from species interactions, illustrated in Figure 3.2. Positive effects generally derive from obtaining resources, usually food, from another. Negative effects derive from losing resources to another, either by being eaten or as a result of the effort expended in obtaining resources. Positive effects promote the survival of individuals and populations. Negative effects may be harmful to individuals and even to populations, but may not be harmful from a long-term survival or evolutionary viewpoint. An interaction that yields a negative effect on at least one participant is termed here 'antagonistic'.

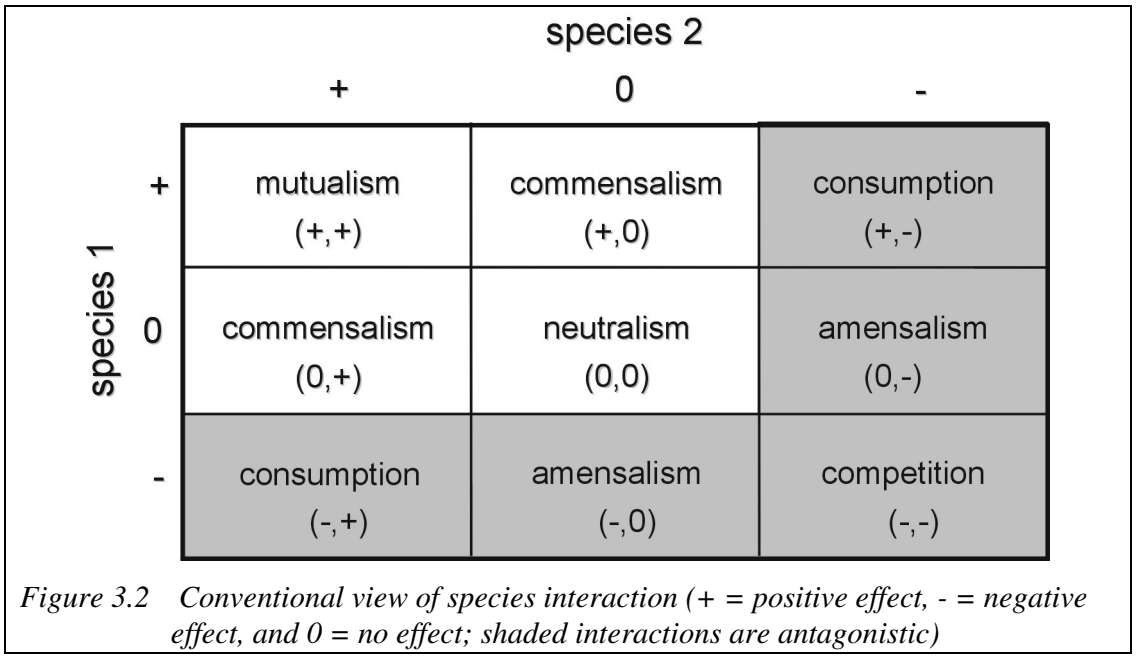


Figure 3.2 Conventional view of species interaction (+ = positive effect, - = negative effect, and 0 = no effect; shaded interactions are antagonistic)

Examples of coevolution may be found for the interactions located at the four corners of the matrix in Figure 3.2. Consumption encompasses interactions typically involving species from different feeding (trophic) levels in the food chain. It should not be confused with its economic meaning. Here it refers to antagonistic interactions where one species purloins resources by eating (parts of) another. Thompson (1994) distinguishes:

- parasites – species that complete an entire stage of development on a single *host* individual and may cause some decrease in fitness of this host;
- grazers – species that move among and feed on two or more individual *victims* without necessarily killing them; and,
- predators – species that rapidly kill and eat individual *prey*.

Box 3.1 provides examples of coevolution triggered by consumptive interactions.

Box 3.1 Examples of coevolution from consumptive interactions

Parasite-host

Vertebrate immune responses to parasitic ticks include inflammation at the site of the bite, which prevents the tick from obtaining a blood meal, and antibodies that bind with proteins in the mite's saliva and prevent it from feeding effectively. In turn, ticks have developed an impressive array of mechanisms to overcome host immunity, including substances in the saliva that act as anticoagulants and prevent inflammation responses (Wikel & Bergman 1997 in Proctor & Owens 2000)).

Grazer-victim:

The original example of coevolution identified by Ehrlich and Raven (1964) – butterfly larvae and the plants they eat – falls into this category. Plants produce novel chemical compounds (secondary compounds or allelochemicals) that reduce the palatability of the plants to plant-eating insects. A new mutant or recombinant then appears in an insect population that is able to overcome the novel plant compounds.

Predator-prey:

Bshary and Noë (2000) examined the development of reciprocal behavioural strategies between a predator (chimpanzees) and prey (red colobus monkeys) in the Tai National Park, Ivory Coast. The red colobus usually move away silently through the canopy when chimpanzees appeared. However, if a group of diana monkeys was nearby, red colobus sought their presence even if they had to move towards the chimpanzees. Diana monkeys post sentinels to look out for predators approaching over the forest floor. Chimpanzees refrained from hunting the red colobus if they were associated with Diana monkeys.

Competition refers to antagonistic interactions when parties strive for the same thing. It may occur among individuals of the same species (intraspecific) or of different species (interspecific). The focus here is on the latter. Unlike consumption and mutualism, competition may occur without participants coming into direct contact. For example, they may be using a common resource in short supply such as food, water, or space. Competition for food is common, and so many instances of competition are intra-trophic interactions. Examples of coevolution from competition are provided in Box 3.2

Box 3.2 Examples of coevolution from competitive interactions

Diamond (1986) studied closely related pairs of bird species in New Guinea. Only with significant geographical overlap (sympatry) these pairs differ in body size or in food source. This suggests character displacement following the partial allopatric model (see Section 3.3.3), and that competing species were coevolving.

The seminal work of Grant (1986) and Grant and Grant (1989) demonstrated that both character displacement and differential colonisation were involved in the coevolution of Galápagos finches. These authors and their colleagues linked differences in species to competition for food.

Adams and Rohlf (2000) report ecological character displacement between two salamander species, *Plethodon cinereus* and *P. hoffmani*. No morphological or resource use differences were found between allopatric populations, while significant morphological differentiation was found between sympatric populations. The major differences were related to differences in jaw closure, which can be linked to differences in prey.

Mutualisms are usually, but not always, inter-trophic interactions where both partners enjoy a net benefit. Originally thought to be altruistic, this interaction is now generally recognised to be based on mutual exploitation for mutual reward (Bronstein 1994). Indi-

viduals accrue fitness benefits from the association compared with individuals not engaged in the association (Stearns & Hoekstra 2000). Mutualisms vary from obligate, species-specific associations to looser, more generalised interactions, and from species living in close association for their entire lifetimes to free-living species. The term 'symbiosis' is often used as a synonym for mutualism, but this dissertation follows Bronstein (1994) and others in defining symbiosis as any morphologically and physiologically intimate relationship, whether or not it yields a benefit for both participants. Box 3.3 provides examples of coevolution within mutualisms.

Box 3.3 Examples of coevolution from mutualistic interactions

Attine ants and their fungal gardens

The tribe Attini includes leaf-cutting ants that strip foliage from plants, carrying it back to their nest where it is used as a substrate for growing fungi in underground gardens. The fungi are the primary food source for the ants. Each species of leaf-cutting ant lives in a symbiotic and mutualistic relationship with its own species of fungus; the relationship is, as far as is known, obligate. Hinckle *et al*. (1994) showed that present-day species of ants and fungi are the product of coevolution over some 50 million years from a single, ancestral ant-fungus symbiosis, although strict co-speciation of ants and fungi appears to be relatively recent (Chapela *et al*. 1994).

Yuccas and the yucca moth

Yucca moths use specialised mouthparts to collect pollen from yucca plants. They lay their eggs in the ovary of yucca flowers by cutting into the ovary with an ovipositor. The moths then walk up the stigma and actively deposit pollen, ensuring the availability of developing seeds. These seeds are the exclusive food of their offspring although the larvae consume only a small proportion. Oviposition attempts and pollination may be repeated. Coevolution is indicated not only by specialisation in flower shape and pollinator's mouthparts, but also by the moth's behaviour in actively pollinating the flower (Pellmyr & Huth 1994).

Frugivores and fruit

Coevolutionary, mutualistic relationships are not always obligate, nor even pair-wise. The reciprocal relationship may be between two groups of species sharing two general traits. The basic pattern in the interaction between fruit-bearing plants and fruit-eaters or frugivores (Janzen 1997) is an example. The frugivore gains food, the plant gains dispersal of its seeds.

Insects and symbiotic bacteria

Wu *et al*. (2006) provide an example of genomic coevolution. Mutualistic intracellular symbiosis between bacteria and insects is a widespread phenomenon that has contributed to the global success of insects. A cicada, the glassy-winged sharpshooter (*Homalodisca coagulata*), has two bacterial symbionts that live in specialised tissue of the host know as the bacteriome. This cicada feeds on plants' xylem sap, which is very poor in organic nutrients including amino acids and vitamins. Phylogenetic studies have shown coevolution of the sharpshooter with two bacteria belonging to very different prokaryotic lineages and with hardly any overlap in biosynthetic pathways. One can synthesise amino acids and the other can synthesise cofactors and vitamins.

Consumptive, mutualistic and competitive interactions may trigger fitness costs and/or benefits on participants. An organism suffering costs is at risk from the interaction and so subject to selective pressures to reduce costs. An organism enjoying benefits may be under selection to obtain more benefits. Sections 3.3-3.5 address each of these interactions with the aim of identifying the various evolutionary processes that have been 'employed' to reduce the costs and increase the benefits from interaction.

3.2.3 Evolutionary paths triggered by interaction

Figure 3.2 pictures the interactions between species as either static or in equilibrium. This is a very limited view given that the outcome of any interaction can vary with, or is conditional on, ecological setting, life history stage and population size (Bronstein 1994). Interspecies interactions can trigger adaptation that may change an interaction from one type to another. For example many mutualisms involve the consumption of one species by another, and are presumed to have begun as a consumptive interaction (e.g. Mack 2000). It is these processes that are the prime interest of this chapter. These two points – static versus dynamic, conditional outcomes – are depicted in Figure 3.3.

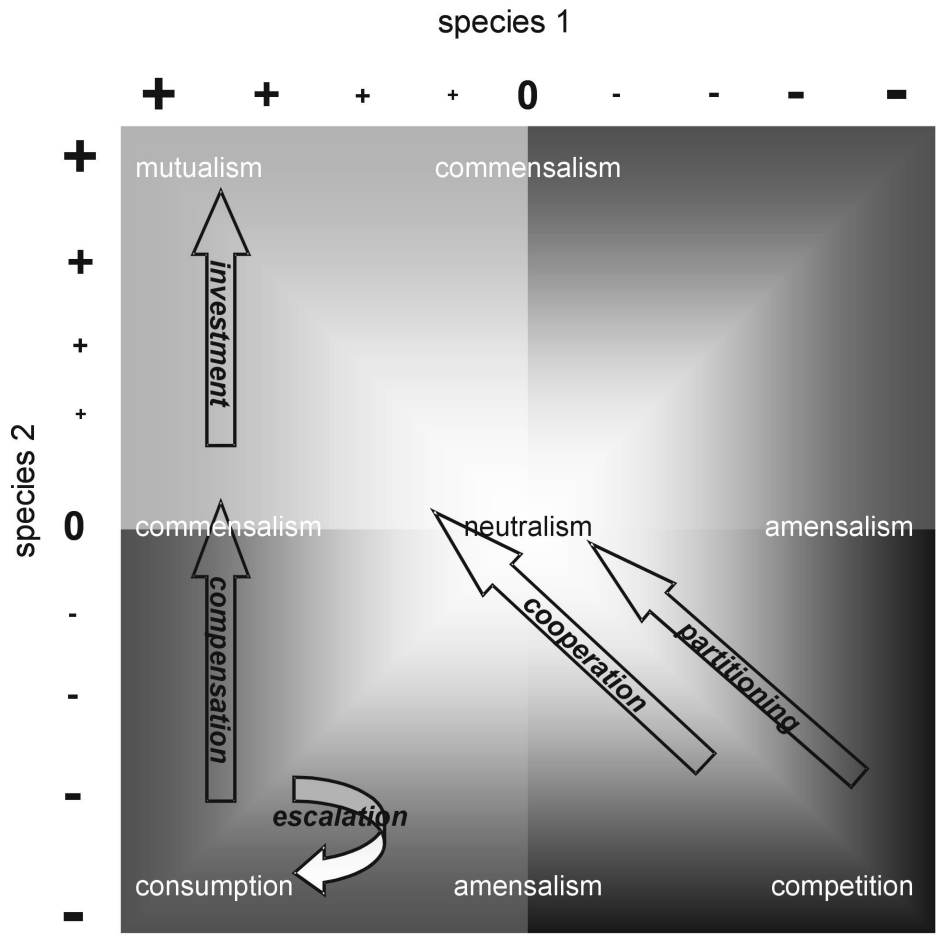


Figure 3.3 Gradations in outcomes of species interaction and the evolutionary processes interaction may trigger (+ = fitness benefit, - = fitness cost, 0 = neither fitness benefit nor cost)

Figure 3.3 repeats the interactions shown in Figure 3.2. Here the pluses and minuses relate to longer term fitness benefits and costs on populations and species, not just the immediate effects of interaction. These effects grade from extremely high costs and benefits (large size of pluses and minuses) to relatively minor costs and benefits (small size). Fitness costs to both participants are shaded black; fitness costs to one participant are shaded dark grey; fitness benefits to both participants are coloured light grey; and no

costs or benefits is coloured white. The gradation in colours reflects difference magnitudes of costs or benefits.

Figure 3.3 also depicts, as arrow, five evolutionary processes, identified from the literature, that interaction may trigger: escalation, compensation, partitioning, cooperation and investment. Escalation maintains the interaction, although its strength may vary. The remaining processes change the outcome of an interaction over evolutionary time. Three reduce antagonism, and one reinforces mutual net benefits. The arrows in Figure 3.3 indicate the net direction of change. They should be seen more as 'slippery slopes' rather than steady, unidirectional change. Changes in outcome are unlikely to proceed smoothly over time, and may suffer reverses, perhaps as a result of changed ecological conditions or because initially promising adaptations fail to improve fitness in the long term.

The figure does not mean to suggest that mutualisms are the ultimate outcome of coevolution. While some species have achieved a mutualistic relationship, most species are subject to so many sources of selection pressure that the evolution of a mutualism would seem unlikely. Once the fitness costs induced by an interaction with another species are reduced, other sources of fitness pressure may come become more urgent and drive subsequent evolution. There are questions as to the stability of mutualistic relationships. Most mutualisms, perhaps all facultative mutualisms, have displayed different outcomes under different conditions (Bronstein 1994; see discussion below). They are also subject to parasitism, where a third species intercepts the exchange of benefits between partners (Yu 2001). Finally, species may be constrained in their ability to generate appropriate adaptations. For example, not all species are capable of making the transition from free-living to captive status as required for domestication (Price 1999). Each of the five evolutionary processes in Figure 3.3 is discussed below.

3.3 Evolutionary processes and mechanisms

3.3.1 Escalation

Escalation occurs within some consumptive interactions. The consumed host, victim or prey may be subject to selection for improved defensive adaptations to reduce the fitness costs of being consumed by a parasite, grazer or predator (Freeman & Herron 1998). Escalation occurs if the consumer then responds with an adaptation to counter such defence (see Figure 3.4). The original illustration of coevolution (Ehrlich & Raven 1964) is an example of escalation, as are the examples in Box 3.1. The term ‘escalation’ is offered instead if more dramatic or esoteric terms found in the literature, such as evolutionary arms race (Dawkins & Krebs 1979; Bshary & Noë 2000; Hedenström & Rosén 2001) and the Red Queen Hypothesis (Van Valen 1973). The latter term derives from Lewis Carroll's “Through a Looking Glass” where the Red Queen says to Alice: “Now, here, you see, it takes all the running you can do, to keep in the same place".

Escalation always involves reciprocal adaptation and coevolution. It is characterised by adaptation by one participant that counters an adaptation by the other participant in the interaction. Counter adaptation is followed by iterations of defensive adaptations and their neutralisation, as indicated in Figure 3.4. The overall result of these iterations is that antagonism is maintained – despite evolving as fast as they can, participants do not

change their relative positions. It is possible that escalation is more prevalent in predator-prey interactions where contact is short-lived (Thompson 1999c).

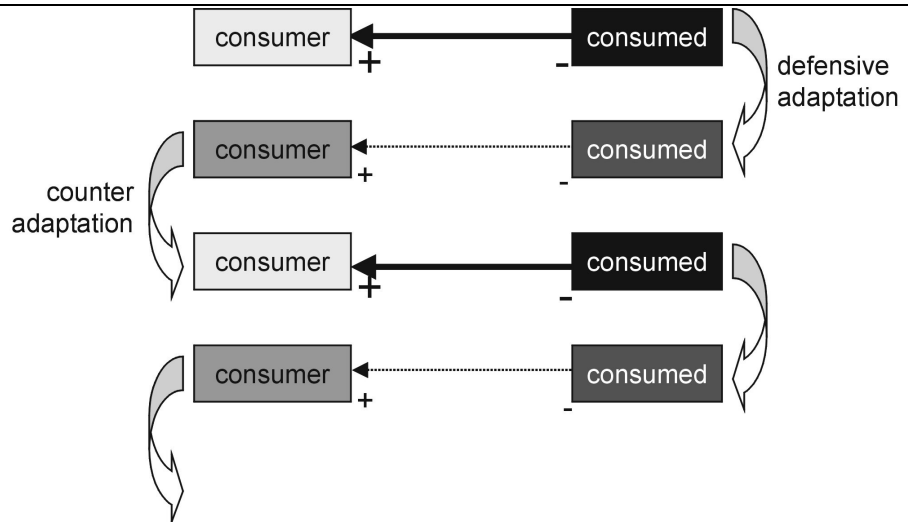


Figure 3.4 Escalation between consumer and consumed, initially, consumption causes large fitness costs to the consumed and large fitness benefits to the consumer; defensive adaptation reduces costs to the consumed; reduced benefits to the consumer triggers a counter adaptation which ensures sufficient benefits to the consumer but engenders costs to the consumed; iterations of defensive and counter adaptation ensue

Escalation threatens to destabilise the interaction (Abrams 2000) and so may preclude long-term co-existence. An example of escalation involving social systems is the resistance of insects and bacteria to pesticides and antibiotics. The maintenance of antagonism and the threat to long-term co-existence mean that escalation is an undesirable evolutionary process from an anthropocentric perspective.

3.3.2 Reduced antagonism through compensation

Consumption is conventionally viewed as an antagonistic interaction over evolutionary (many generations) as well as ecological time (one or few of generations). A more recent perspective highlights that there are circumstances in which benefits can be gained from being consumed. Further, selective pressures can reduce antagonism over evolutionary time, and bring about a shift from consumption towards commensalism and even mutualism (Bronstein 1994, and see Figure 3.5). Sufficient data now exist to show that plants commonly display compensation to herbivory – derive benefits from herbivory to compensate for its costs – such that the removal of plant tissues by herbivores may not reduce plant fitness (Strauss & Agrawal 1999; Agrawal 2000; Stowe *et al*. 2000). Examples include release from apical dominance and phenological escape (Agrawal 2000).

Similarly, parasites are not always bad for the host and, under certain conditions, may even be of benefit (Michalakis *et al*. 1992, Thomas *et al*. 2000, Herre *et al*. 2000). Examples where parasites are of benefit to their hosts include (Thomas *et al*. 2000):

- host is avoided by predators and cannibals when parasitism is advertised, presumably because of the risk of infection;
- infection by less harmful parasites can reduce infection by more virulent ones;

- early exposure to a parasite builds naturally-acquired immunity to infections whose detrimental effects increase with age (e.g. mumps or *Parotitis epidemica*);
- host enjoys less competition when parasite is more pathogenic to competitors;
- females choose mates who can demonstrate resistance to parasitic infection; and
- adverse environments, where parasites may act as internal sinks for toxic substances;
- parasitised individuals may be fitter under deficient dietary conditions, as shown for ground squirrels, *Spermophilus richardsonii,* parasitized with the protozoan, *Trypanosoma otospermophili,* when their diet was deficient in pyridoxine (vitamin B6).

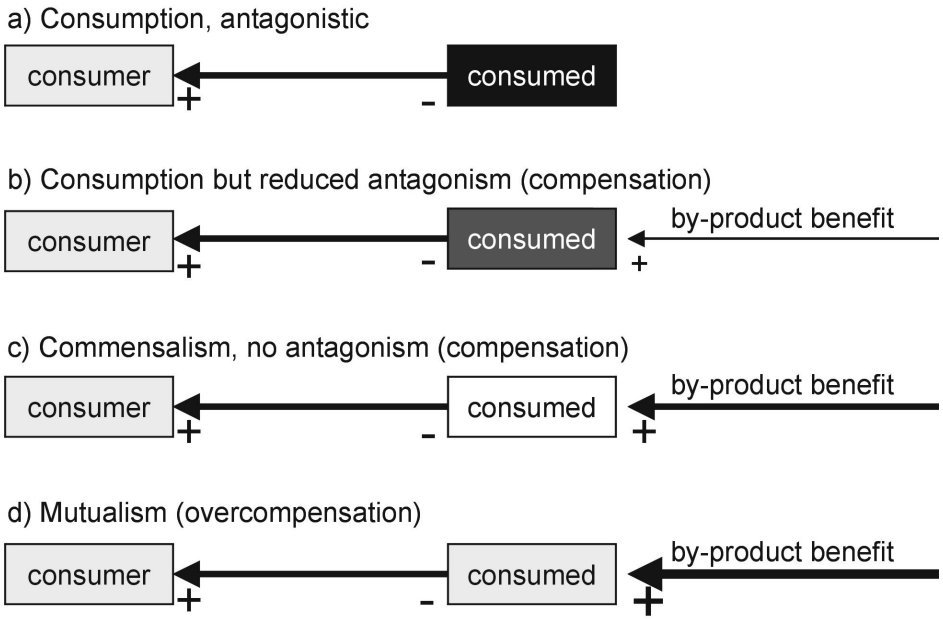


Figure 3.5 Compensation reduces antagonism: a) the original interaction where the consumer enjoys benefits (light grey) and the consumed suffers costs (black); b) compensation where the net costs to the consumed are reduced by by-product benefits (dark grey); c) costs to the consumed have been negated by by-product benefits (white); d) by-product benefits exceed costs to the consumed (light grey) and the interaction has become mutualistic with net benefits to both participants

This suggests an alternative evolutionary process to escalation, in which individuals are selected that derive benefits to compensate for, or offset, fitness costs. These benefits are termed 'by-product benefits'. By-product benefits result from a selfish act by one species that inadvertently produces a net benefit for a second species (Brown 1983). Unlike escalation, this evolutionary process is capable of reducing antagonism in the long term. It may also offer a way to avoid escalation (Michalakis *et al*. 1992). Compensation does not necessarily lead to coevolution because adaptations by the consumed to compensate for the costs of consumption may not induce a reciprocal response by the consumer.

Compensation pushes a consumptive interaction towards commensalism, at which point the costs of interaction are balanced by benefits. It may also push the interaction beyond commensalism so that the initially disadvantaged participant comes to enjoy a net benefit. This is termed overcompensation in the context of plant responses to herbivory (Strauss & Agrawal 1999; Agrawal 2000). By reducing the costs of interaction, facilitat-

ing co-existence, and with the potential for yielding mutual net benefits, this evolutionary process is considered desirable from an anthropocentric perspective. The mechanism behind this process is the generation of by-product benefits.

3.3.3 Reduced antagonism through Partitioning

Competition is an antagonistic interaction that can induce fitness costs on all participants. It can result either in the exclusion of the less competitive species over ecological time, or in the ecological separation of the competitors over evolutionary time. The former precludes the coexistence of competitors while the latter facilitates it. Natural selection triggered by competitive interactions focuses on cost avoidance, on precluding the interaction. This makes competition fundamentally different from consumption. Selection within consumptive interactions favours reduced interaction for one participant but increased interaction for the other. Consumptive interactions are held together because one species is pursuing the other in evolutionary time (Thompson 1999c).

Partitioning is the evolutionary process that reduces antagonism and achieves ecological separation. It pushes the participants apart and the interaction towards neutralism (see Figure 3.6). Three types of partitioning can be identified:

1. resource partitioning occurs when competitors come to use different parts of the same resource (e.g. leaves versus bark of a tree);
2. spatial partitioning occurs when competitors come to use the same resource but in different places (e.g. high versus low altitudes);
3. temporal partitioning occurs when competitors use the same resource but at different times (migratory patterns of the large herbivores of the savannah – Graham & Lundelius 1984).

A fourth type of partitioning – scale partitioning – is also possible, with the same resource being used by competitors of different body sizes (Ritchie & Olff 1999). Box 3.4 provides examples of each type of partitioning from social systems. These examples are not meant to imply subsequent evolution or coevolution.

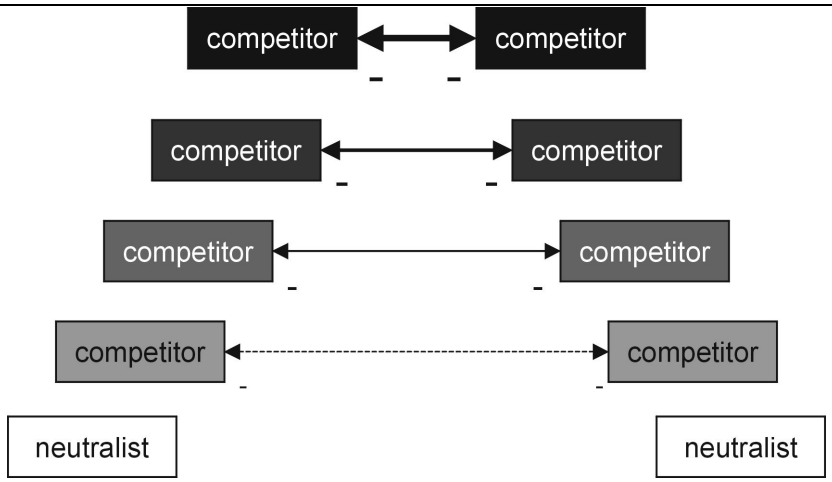


Figure 3.6 Character displacement pushes competitors apart by reducing the intensity of competition (indicated by darkness of colour), avoiding associated costs and pushing the interaction towards neutralism (white)

Partitioning may not necessarily lead to reciprocal adaptation. The coevolution of competitors is clearest with speciating congeners. Two populations of the same species may diverge while allopatric. This divergence accentuates characters affecting reproduction, and so separates the populations into distinct species. When species become sympatric, perhaps as a result of landscape change, competition forces ecological separation (Diamond, 1986). Characters associated with habitat or resource use are accentuated in this second divergence and probably involve reciprocal adaptation of both species. The underlying mechanism is termed character displacement. While various studies support this partial allopatric model, care should be taken as examples of character displacement can often be explained by other hypotheses (Levinton 1982; Grant 1994).

Box 3.4 Examples of the partitioning between social competitors

Resource partitioning

The iron-and-steel industry and power generation both use coal. The former can only use high quality coal for coke production. Technological development over the last 30-50 years has permitted coal-fired power plants to make use of poorer quality coal. Competition has been avoided, and co-existence facilitated.

Spatial partitioning

This is a common strategy, typified by land use planning and land ownership to reduce competition for land among agriculture, industry, residential and infrastructure development, and nature conservation. Various strategies are used to allocate rights of access and use of resources such as freshwater, subsoil resources, forests, and rangelands.

Temporal partitioning

This can be seen in price differentials for using a resource at different times. Examples are off-peak hot water systems, cheaper matinee tickets for theatre performances, and penalties for travelling during peak hours.

Scale partitioning

Compare supermarkets and speciality shops. Large supermarkets offer a high diversity of relatively cheap products; smaller speciality shops offer a smaller range of better quality goods at a higher price.

Partitioning promotes the co-existence of competitors by selecting for adaptations that avoid the costs of interaction and reduce the risk of competitive exclusion. This process pushes the outcome of interaction towards neutralism and it would seem unlikely that the outcome would be pushed further towards mutualism. However the migratory patterns of herbivorous megafauna in the African savannahs, the example above of temporal partitioning, suggests that this is possible. Graham and Lundelius (1984 – various references cited) describe a situation in which the grazing by each herbivore wave stimulates the growth and development of plant species or plant parts such that food resources are available for subsequent waves. The evolutionary outcome from this (originally) competitive interaction is not neutralism, but a complex, multi-species mutualism.

Partitioning may be considered desirable from an anthropocentric perspective because it promotes co-existence even though mutual net benefit would seem unlikely. The mechanism is ecological separation.

3.3.4 Cooperation

The study of cooperation in ecology is usually restricted to competitive intraspecific interactions (Bronstein, 1994). Cooperation, elaborated here as an evolutionary process, stems from interspecific competitive interactions. Mixed herds, flocks and schools are examples of cooperation among competitors and may have developed as a better solution to common problem (Thompson 1999c). The costs of competition are outweighed by, say, more efficient resource use or reduced predation, which are brought about by the by-product benefits of association. The amount of benefit from cooperation will vary with the severity of the common problem, which in turn may vary over time and space. For example, mixed herds with improved predator warning will enjoy large by-product benefits when predators are abundant; when predators are absent, such aggregations will serve only to increase competition. Cooperation is illustrated in Figure 3.7.

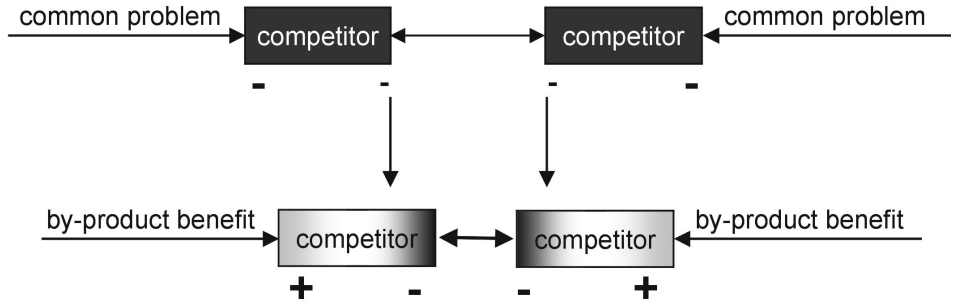


Figure 3.7 Cooperation in the face of a common problem brings competitors closer together, with the outcome dependent on the severity of the problem and the amount of by-product benefit derived; greater competition (dark grey to black), neutralism (dark grey to white) as by-product benefits offset competition; or a light mutualism (dark grey to light grey) with by-product benefits exceeding fitness costs

The seminal work of Trivers (1971), Axelrod (1884) and Hamilton (Axelrod & Hamilton 1981) examined the evolution of cooperation using a game called the Iterative Prisoner's Dilemma (IPD – see Box 3.5). The game provides a means for examining the persistence of cooperation in a non-cooperative world. It has spawned an avalanche of papers, but the applicability of much of this work in the context of biological systems is limited (Brembs 1996). The emphasis has tended to lie with theoretical models and not with empirical corroboration by which IPD could be linked to known situations of cooperation. IPD is limited in its ability to explain cooperation among the vast majority of biological entities that are generally incapable of strategic behaviour – they cannot recognise past players, remember their past actions, or anticipate future encounters. The possibility of incremental building on cooperation is not captured, nor does IPD permit a realistic representation of retaliation that probably responds to different degrees of cheating. Finally, IPD does not offer a mechanism to explain the initial viability of cooperation.

Game theory has been successful in the social and economic sciences, both in terms of its theoretical insights and its potential relevance for policy-making (e.g. Folmer & Zeeuw 1999). It has been used to model a variety of problems in environmental economics such as property rights and externalities, bargaining, free-rider behaviour and moral hazard, and international agreements. Brembs' criticism of the use of games in biology is

also pertinent for the social and economic sciences. There is a need to apply game-theoretical notions in an empirical setting.

Box 3.5 The iterative prisoner's dilemma

The Iterative Prisoner's Dilemma (IPD) is a game involving two players who, each turn, may choose to cooperate or to defect. There are four possible outcomes (see below), each of which scores points for the players. The objective is to score the most points.

		PLAYER 2	
		Cooperate	**Defect**
P	**Cooperate**	R=3; R=3	S=0; T=5
L		Both players	Player 1 cooperates
A		cooperate	Player 2 defects
Y			
E	**Defect**	T=5; S=0	P=1; P=1
R		Player 1 defects	Both players
1		Player 2 cooperates	defect

The mathematical constraints on payoffs are given by:

$$T > R > P > S \text{ and } R > (T + S)/2$$

where
T = temptation to defect;
R = reward for cooperation;
P = punishment for mutual defection; and,
S = sucker's payoff.

For a single interaction, or a game with a known number of interactions, the only stable strategy is to defect. This strategy takes advantage of the sucker's payoff and yields an expected mean score of 3 (*cf* 1.5 from cooperation). But the same holds for the other player, with the result that individual rationality leads to a worse outcome for both – a score of 1. However if the number of interactions is not known, and the probability of a further interaction is high enough, successful cooperative strategies are possible. Choices made now may influence later choices of players. The future casts a shadow on the present, thereby influencing the current strategic situation.

Axelrod (1884) and others have tested a wide range of strategies or decision rules that specify what a player does in any given situation. ALL D is the strategy based on individual rationality with the player defecting on all moves. The most famous cooperative strategy is tit-for-tat (TFT) in which a player cooperates on the first move then copies the previous move of the other player on each subsequent move. This strategy is based on 'reciprocity'. Its success stems from the benefits of repeated interactions with other cooperators – receiving the R payoff and avoiding more than one S payoff.

In facilitating the co-existence of competitors and with the potential of yielding mutual net benefit, cooperation is considered desirable from an anthropocentric perspective. The mechanism lying behind this evolutionary process is by-product benefits.

3.3.5 Investment

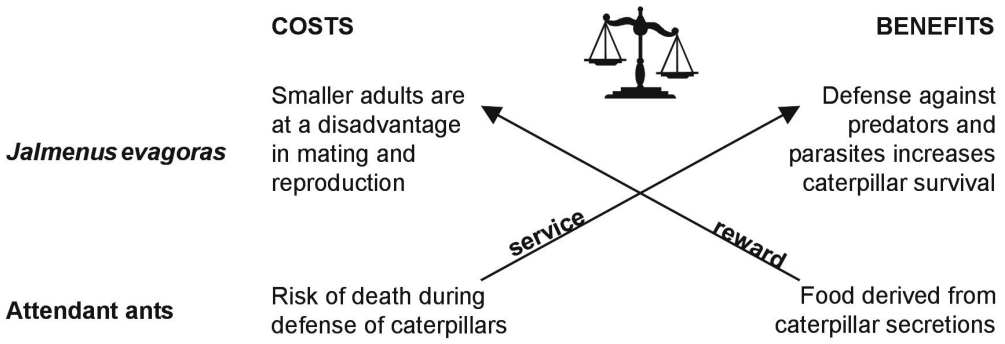
Coevolution is strongly implied in mutualisms. Many mutualisms pair costs and benefits (see Box 3.6), with one participant providing a costly service in exchange for a beneficial reward in the future. In parallel with the conventional meaning, this is termed investment (Connor 1995). Benefits must exceed costs, at least in some situations, for the mutualism to persist. Mutualisms are dynamic interactions that may not always result in

mutual benefit. The outcome is contingent on life history stage, population size and ecological setting such that it is sometimes mutualistic, sometimes commensal or even antagonistic (Cushman & Whitham 1989; Cushman & Addicott 1991; Cushman & Whitham 1991). Conditional outcomes have been documented for every form of facultative mutualism studied to date (Bronstein 1994).

*Box 3.6 The mutualism between a lycaenid butterfly (*Jalmenus evagoras*) and its attendant ants* (Pierce 1984, Pierce *et al.* 1987)

The interaction between lycaenids and attendant ants takes a variety of forms. In one form, caterpillars of the lycaenid butterfly *Jalmenus evagoras* possess glands that exude a fluid containing sugars and amino acids. This fluid is apparently consumed by the ants that tend the caterpillars and defend them against predators and parasites. Caterpillar mortality for those with attendant ants is lower than for those without attendant ants.

Each provides a benefit to the other (food or defence), but at a cost. This is shown in the figure. Ants defend the caterpillars at considerable risk to their own lives. Butterfly adults are smaller, probably because resources are redirected from growth towards feeding attendant ants. Smaller butterflies are at a disadvantage in mating and reproduction.



The persistence of this mutualism over evolutionary time implies that both participants enjoy a net benefit relative to those individuals living apart. The persistence of caterpillars without attendant ants indicates the difficulty that ants and caterpillars have in finding each other (a common problem for many mutualisms – Yu 2001), and/or the net benefit is conditional (see Section 3.3.2).

Mutualisms have excited much discussion with regards to how they evolved and how they persist (e.g. Bronstein 1994; Agrawal 2000; Yu 2001). The verbal model of Connor (1995) conceptualised the exchange of benefits by participants in a mutualism. In short, a light mutualism based on by-product benefits accruing to one or both participants must already exist. One partner comes under selection to derive more benefit from the interaction. Its adaptations lead to investment in the benefits accruing to the other; the partner under selective pressure performs costly acts in the hope of increasing the probability of receiving benefits in return. Figures 3.8 and 3.9 show possible routes for investment.

In Figure 3.8, the basal mutualism involves a consumer enjoying the benefits of consumption, and a consumed accruing by-product benefits that offset the costs of consumption. This was also termed overcompensation in Figure 3.5. The shading in Figure 3.8 indicates the conditional nature of these by-product benefits and thereby of the outcome from the interaction. Step 1 in Figure 3.8 assumes that the consumed species needs to derive more benefits from the interaction. One adaptive response could be to invest in the

consumer, anticipating that this will generate additional by-product benefits. To illustrate, fruit could represent investment in frugivores that, in the course of eating a plant, happen to disperse its seeds. This dispersal is a by-product benefit to the plant. The frugivores derive more benefits from eating the fruit. If, as a result, there is more or more reliable dispersal of seeds, then the plant has increased the by-product benefits it derives from the interaction. If these benefits exceed the costs of making fruit, as well as reducing selection pressures, the adaptation is likely to persist.

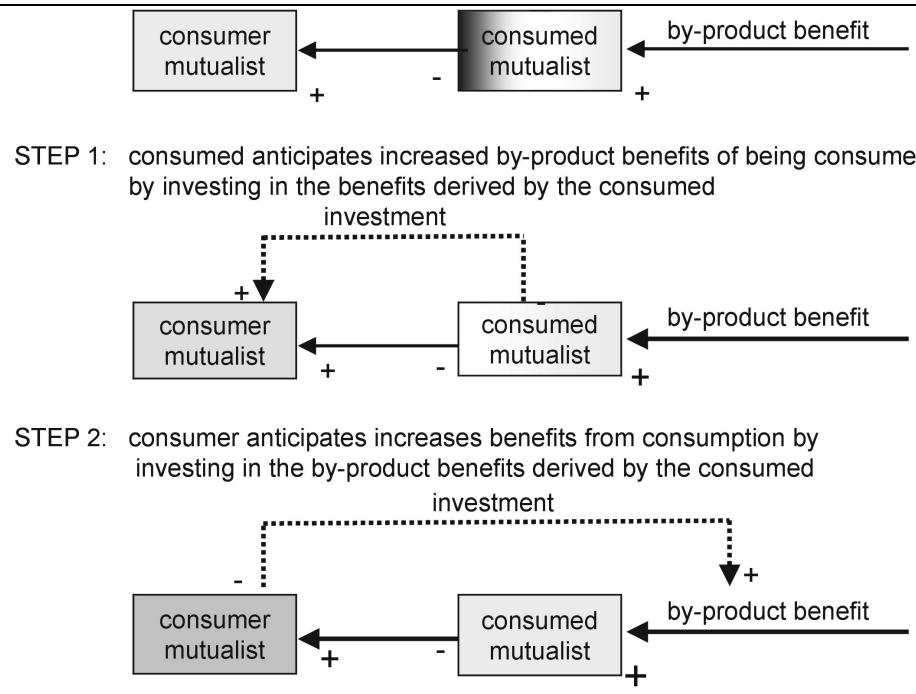


Figure 3.8 Investment in a basal mutualism based on consumption with by-product benefits; investment is stimulated by selective pressure on the consumed mutualist to incur fewer costs;

Should the consumer subsequently come under selection to derive more benefit from the interaction, it may also adapt by investing in the by-product benefits of the consumed. To continue the illustration from above, frugivores that deliberately, instead of incidentally, disperse seeds display an adaptation that invests in their partner. Again, such adaptations are more likely to persist if the consumer reaps sufficient benefits from the interaction to compensate for its investment and redress selective pressures.

The two steps shown in Figure 3.8 may occur in the reverse order, with investment by the consumer preceding investment by the consumed. Connor (1995) provides examples of mutualisms showing investment by participants in consumptive interactions.

Figure 3.9 illustrates how investment could occur in a basal mutualism involving a competitive interaction. It begins with a light mutualism in which by-product benefits accrue to both partners, for example from cooperation, and offset the costs of competition. The outcome is conditional on various factors, as indicated by the shading in Figure 3.8. Step 1 assumes that one species comes under selection to increase its net benefits. Adaptations invest in the by-product benefits of its partner, in anticipation that partner will, in turn, reciprocate. Step 2 shows that investment may be reciprocated.

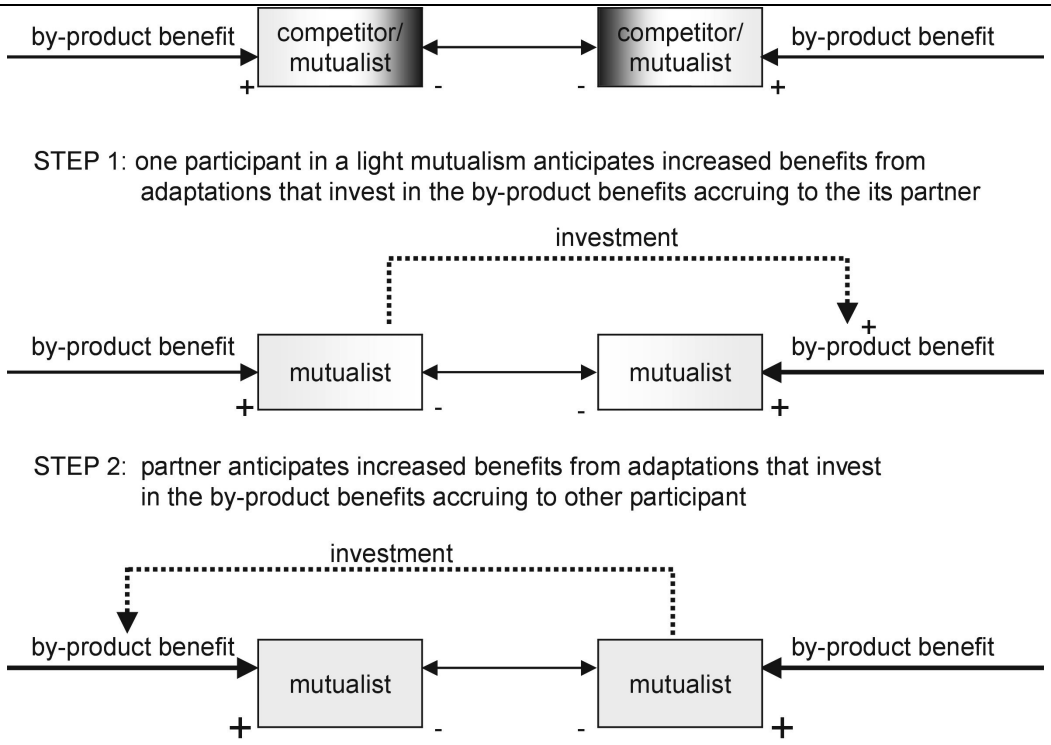


Figure 3.9 Investment in a basal mutualism based on competition

Connor (1995) illustrates investment with a form of artisanal fishing in Mauretania. The fishermen catch mullet using hand-held nets. Once a school of mullet has been sighted, a fisherman wades into the water and hits the water surface with a stick. This calls dolphins that herd the fish against the net barrier. Both dolphins and the fishermen feed from the fish caught and so benefit from their cooperation. The fishermen have invested in the by-product benefits to the dolphins by 'calling' them. Both dolphins and fishermen catch more fish and so enjoy increased benefits. The dolphins have not invested in the interaction. However such investment can be envisaged; for example, they could 'call' the fishermen, or herd the mullet even when not hungry. Again, such adaptations are most likely to persist if the benefits derived from investment outweigh costs and reduce selection pressures.

Connor emphasises that investment, in reinforcing a mutualism, does not change the outcome of the interaction but it may change the character of the mutualism so that its origins become obscured. The 'coinage' of a mutualism may change over evolutionary time so that the benefits that initiated the mutualism might have long since disappeared. To illustrate, Connor offers two alternate means by which ants and acacias have developed their obligate mutualism.

The original, light mutualism was based on by-product benefits that the ants conferred on the plants by eating herbivorous insects. The plants invested in the ants by developing extrafloral nectarines, providing them with food. With this food source, the ants no longer needed to eat the herbivores and so came to merely tossing them off the plant. The original by-product benefits have been lost. Alternatively, the plants disrupted a mutualism between ants and insects, something along the lines of the lycaenid-ant mutualism in Box 3.6. This mutualism supported herbivory. The development of extrafloral

nectaries provided the ants with an alternative, and apparently preferable, food source. They no longer serviced the insects, and even came to removing them from the plant.

Investment as an evolutionary process does not change the outcome of an interaction but serves to strengthen it and to provide greater guarantees of mutual benefit. In promoting co-existence and mutual net benefit, investment is a desirable evolutionary process from an anthropocentric perspective. Investment also carries risks such as cheating, parasitism, misinterpretation, and increased vulnerability.

Cheating occurs when partner does not reciprocate, or does not reciprocate appropriately to compensate for costs. Yu and Pierce (1998) describe the breakdown of an ant-plant mutualism that has led to castration of the plant host (*Cordia nodosa*) by its primary ant mutualist, *Allomerus cf. demerarae*. These ants protect new shoots from herbivory, but at the same time attack and destroy floral buds and so reduce fruit production.

Parasitism of a mutualism occurs when a third party intercept the benefits being exchanged. Examples include nectar-robbing birds that eat a flower's nectar without pollinating it, and ants that feed from extrafloral nectories without defending the plant against herbivores. Yu (2001) discussed possible types of retaliation that could constrain cheating and parasitism, and so guarantee benefit exchange. However, such strategies complicate matters considerably.

It is possible to misinterpret mutualisms. An apparent exchange of benefits may turn out not to be so. For example it has generally been assumed that the interaction between red-billed oxpeckers (*Buphagus erythrorhynchus*) and large African mammals was mutualistic. The oxpeckers glean ticks from the skin of these animals, gaining food for themselves and reducing the impact of the ticks on their hosts. As part of a controlled field experiment, Weeks (2000), to his surprise, found that changes in adult tick loads of cattle were unaffected when the birds were excluded, and that the oxpeckers significantly prolonged the healing time of wounds. This is neither cheating nor parasitism. The interaction between the cattle and the oxpeckers, via ticks, is consumptive and not mutualistic.

Finally, while ensuring mutual benefits, investment can also lead to mutual dependence making participants vulnerable to changes in circumstances. This is best illustrated by current concerns that climate change (see Chapter 2) will disrupt many existing mutualisms and lead to extinction of the participating species. Increased temperatures, for example, may force species to change their geographic ranges. More mobile species may manage this, but are partners in mutualisms equally mobile?

The conclusion is that, while investment may be seen as desirable in an anthropocentric context, the resulting mutualism carries with it considerable risk.

3.4 Coevolution across space

Interactions can yield different outcomes (conditionality) as a result of differences in the physical environment, the local genetic and demographic structure of populations, and the community context in which the interaction occurs. Conditionality means that an interaction may lead to coevolution in some populations, affect the evolution of only one participant in others, and have no effect on evolution in yet other populations. Interpopulation differences in outcome create a geographic mosaic in interactions and their evolu-

tionary consequences. The overall evolution of a species is likely to be the product of coevolution with several species, even though individual populations interact with only one or two. The situation is further complicated by gene flow, genetic drift, and population dynamics if populations exist as metapopulations.

The geographic mosaic of Thompson (1994; 1999c; & Cunningham 2002) combines metapopulation ecology with biotic interaction to study coevolution across space. In a metapopulation, a selection mosaic exists that may lead to different evolutionary trajectories in different subpopulations. The combination of a selection mosaic, gene flow among and genetic drift within populations, and local extinction and recolonisation of subpopulations (basic metapopulation dynamics) creates a continual geographic remixing of the range of coevolving traits. Thompson (1999c) makes three ecological predictions from this mosaic. Prediction and evidence for them are summarised in the following section.

Firstly, subpopulations will differ in the traits shaped by an interaction. Not only do traits differ, but they may display clines or mosaics across landscapes in terms of the proportion of individuals harbouring the traits (Kraaijeveld & Godfray 1999; Lively 1999). Some coevolved traits of an interaction are maintained only or primarily through connections among subpopulations (Burdon & Thrall 1999). Further, differences among subpopulations in the intensity of selection on coevolved traits, and so the coevolutionary trajectory, differs across the communities (i.e. assemblages of populations) in which the interaction occurs (Benkman 1999).

Secondly, traits of interacting species will be well matched in some communities and mismatched in others, producing some cases of local maladaptation. Benkman (1999), Burdon & Thrall (1999), Lively (1999), and Parker (1999) report instances in which gene flow among subpopulations created local maladaptations, and prevented or swamped local coevolution in some communities.

Thirdly, there will be few species-level coevolved traits (i.e. coevolved traits that are distributed across all populations of a set of interacting species), because few coevolved traits will be favoured across all communities. The point of this prediction is that few coevolved traits will ever become fixed in coevolving species, and so it addresses the general view of coevolution as a ‘rare event’. Thompson is arguing that coevolution plays a much more important, if not integral, role in the evolution of species even though it only becomes visible in a small proportion.

The overall evolution of the species could well be the product of interaction with several species, even though subpopulations interact with only one or two (Thompson 1994). The geographic mozaic allows for the evolutionary persistence of interactions that would otherwise become unstable (e.g. evolutionary arms races) or extinct, and it may routinely produce local, transient mismatches of traits or maladaptations. It all depends on the respective roles of the three components – selection mosaics, coevolutionary consequences, and trait remixing among populations. The result is a continually shifting geographic pattern of evolution among interacting species in which evolutionary processes need not result in strict reciprocal adaptation nor fixed traits within species.

3.5 Analogies in environmental management

This chapter identified five evolutionary processes from interactions between species. The following discussion draws an analogy between species interactions and interactions between social and natural systems. Specifically it takes an anthropocentric perspective, and assesses the 'desirability' of these five evolutionary processes should they apply to the coevolution of social and natural systems. Desirability was defined in the introduction in terms of two criteria: continued co-existence of participants, and the potential for both participants to derive net benefits. The above discussion of the five processes also touched on their desirability. Table 3.1 summarises this assessment.

Table 3.1 'Desirability' of evolutionary processes in the context of interaction between social and natural systems

Evolutionary Process	Long-term co-existence	Mutual net benefit	Possible constraints	Desirability
Escalation	threatened	no		No
Compensation	yes	possible		Yes
Partitioning	yes	unlikely		Partial yes
Cooperation	yes	yes	requires a common problem	Yes
Investment	yes	yes	builds on an existing mutualism cheating and parasitism	Yes

Escalation is the only undesirable process from an anthropocentric perspective. Defensive adaptations followed by counter adaptations maintain antagonism. Benefits accrue to one participant only. There is potential for escalation to destabilise the interaction and so the long-term co-existence of participants is threatened. The remaining four evolutionary processes are considered desirable to some degree.

Compensation offers an alternative path for consumptive interactions. One partner enjoys benefits from the interaction, while the associated costs incurred by the other are offset by by-product benefits. This process offers prospects for maintaining co-existence as well as the potential for leading to outcomes with mutual net benefit.

Partitioning separates competitors ecologically and evolutionarily. By avoiding antagonism by mean of avoiding interaction, partitioning facilitates co-existence. However it would seem more likely to lead to neutralism, where participants experience neither costs nor benefits, than mutual net benefit, and so only satisfies one criterion of desirability.

Cooperation is an alternative route for competing species, and potentially more desirable than partitioning because it offers the possibility of both co-existence and mutual net benefit. However it is conditional upon the presence of a common problem so that cooperation yields benefits to participants.

These three evolutionary processes cater for a movement away from antagonism when it induces fitness costs. The central mechanism behind two of these processes is by-product benefits, which offset fitness costs. The mechanism behind the third is ecological separa-

tion by character displacement, which leads to the avoidance of fitness costs. The former mechanism, by-product benefits, offers the potential for an outcome that is mutually beneficial, at least under some circumstances. The latter mechanism, ecological separation, is most likely to lead to a situation where participants neither enjoy benefits nor suffer costs.

Investment would seem to be the most desirable of the five processes, given that it reinforces both co-existence and mutual net benefit. However, I would caution such a conclusion. A prerequisite for this evolutionary process is that participants already enjoy mutual net benefits, at least in some instances. This may require that investment be preceded by another evolutionary process such as compensation. Further, mutualisms do not seem to be easy interactions to maintain, although given the prevalence of this interaction, individual mutualists may disagree. Not only is the outcome of many mutualisms conditional, but cheating and parasitism can compromise the exchange of benefits to the detriment of at least one mutualist. No mechanism behind investment has been offered, as I could not identify one from my study of the literature. It may be that there are many, or that our understanding of mutualistic interactions is still too limited. I suspect that investment mechanisms are paired with mechanisms that minimise cheating. Yu (2001) discusses such mechanisms, but evidence of their application is limited.

3.6 From species to system coevolution

Interactions between social and natural systems are diverse, but the environmental problems of recent decades are evidence of antagonism towards nature. This antagonism has led to fitness costs for many components of natural systems. Biodiversity loss has become the catch cry highlighting the impacts of this antagonism. Some of the effects of social antagonism have rebounded on social systems: e.g. the collapse of fish stocks and their socio-economic consequences, the bioaccumulation of toxic substances and their effects on human health, the increasing scarcity of water for drinking purposes, and the expected disruption, particularly of agricultural activities, from climate change. Subsequent adaptation by social systems is used as evidence for the coevolution of social and natural systems, and motivation for a coevolutionary focus in environmental management (Lorenzoni *et al*. 2000a and b). It is grounds for concern that the evolutionary process driving this coevolution might be escalation.

The lessons drawn from coevolutionary biology suggest that mechanisms that reduce antagonism offer the first step towards non-antagonistic, if not mutually beneficial, co-existence. Much is being done within environmental management to reduce antagonism; e.g. the implementation of clean technologies, restrictions and incentives for better agricultural and industrial practices, measures to protect valued species and ecosystems, as well as land use zoning and land management. The de-coupling of economic activities from their environmental impacts presents not only technological challenges, but also social challenges as we move towards better housekeeping practices in economic production and consumption (Vellinga & Herb 1999). My analysis of coevolution between species leads me to conclude that such measures are insufficient, for two reasons.

Firstly, many interactions between the two systems are consumptive, such as the extraction of biotic resources. Consumptive interactions are held together because one party is

pursuing the other in evolutionary time. Social systems are pursuing natural systems to derive the environmental goods (e.g. fish, timber) and services (e.g. maintenance of soil fertility, clean air and water) that support human production and reproduction. Environmental management can reduce the antagonism inherent in our use of environmental goods and services, but it cannot remove it. We shall always need some quantity (and presumably some minimum quality) of these goods and services.

Secondly, interactions between the two systems are also competitive, the most prevalent being competition for space. Competitive exclusion of natural by social systems is constrained, in some countries, by partitioning strategies. The most common form is spatial partitioning, via land ownership and land use zoning. This strategy carries risks. At some future point, increased demands by a growing population could lead to the break down of the partitioning and subsequent exclusion of the competitor. To illustrate, and drawing on the case study in Chapter 7, the effect of Presidential Proclamations 2151 and 2152 in the Philippines was to preserve remaining mangrove ecosystems. However some of the remaining stands are under pressure for conversion to aquaculture. The rationale behind such conversion rests on individuals who stand to make a considerable profit, as well as more general economic concerns such as the need to ensure domestic food supply and to increase export earnings (Gilbert & Janssen 1998).

A coevolutionary perspective would complement environmental strategies with a third, based on by-product benefits to offset the costs of antagonism. Such benefits are termed 'positive externalities' within economic literature. Externalities relate to goods and services that are exchanged outside the market system, usually because they are unpriced. Environmental economics has focused extensively on negative externalities such as waste production, disposal and subsequent pollution. To illustrate positive externalities, consider an orchard owner whose flowers need to be pollinated, and a beekeeper who needs the nectar of flowers for his bees to make honey. The former does not pay for the pollination services of the bees, nor the latter for the harvesting of nectar.

With the generation of by-product benefits to offset the costs of antagonism, the path is paved to move interactions between social and natural systems towards mutualism. The long-term goal for the coevolution of social and natural systems is a mutualism, between the systems and their components. Perhaps more realistically, the short-term goal is the reduction of antagonism with a commensal or neutral outcome.

This chapter has addressed coevolution in its original, biological sense as inherited change that may occur between two interacting species. While lessons are drawn for the coevolution of natural and social systems, 'upscaling' from species to systems' interaction is not straightforward, for at least two reasons. Firstly, understanding of evolutionary processes is based on explaining how organisms evolved into what we see today. It is predominantly backward-looking whereas the context in which we talk of coevolving natural and social systems is very much forward-looking as we ask questions about the sustainability of development. Secondly, evolutionary biologists generally baulk at the notion that system's evolve, let alone coevolve. The individual organism is seen as the vehicle of evolution, rather than higher (e.g. groups of species or ecosystems) or lower (e.g. organs, cells, genes) levels in the biological hierarchy. The following chapter offers a very different perspective on evolution and coevolution.

4. A Systems Perspective of Coevolution

You had to admire the way perfectly innocent words were mugged, ravished, stripped of all true meaning and decency and then sent to walk the gutter ....., although 'synergistically' had probably been a whore from the start."

"Going Postal", Pratchet 2005, p 372

4.1 Introduction

The previous chapter addressed the coevolution of species, or more precisely, the evolutionary processes triggered by species interaction. However the notion that systems may coevolve derives as much from evolutionary biology as from the study of complex systems. 'Up-scaling' from the coevolution of species to the coevolution of systems is not simple. As argued by Winder *et al*. (2005), coevolution is more than co-dynamics. Coevolution of systems implies changes to the properties of systems with concomitant changes to internal structure. It would seem axiomatic that coevolution between systems follows different paths, or has different characteristics, than coevolution between species. This chapter reviews literature with the following aims:

- to take the issue of coevolution a necessary step further and so to elaborate on how natural and social systems might coevolve;
- to assess complex networks as a means of representing the interactions among components of complex systems; and,
- to identify measures of network topology that could indicate system change; and,
- to develop a framework of analysis that will be further elaborated in subsequent chapters.

Chapter 3 argued that interaction was a prerequisite for coevolution between species. It is also a prerequisite for coevolution, whether between complex systems or among the components of complex systems. The two perspectives on coevolution can be very simply contrasted. Coevolution of species focuses on adaptations, tracking back to the interactions that led to their selection so that evolutionary processes and mechanisms can be explained. Adaptations and interactions tend to be viewed in isolation from other sources of selection. Coevolution among components of complex systems is less concerned with individual interactions or adaptations, focusing more on the consequences to all components and to system properties. The components of complex systems interact with each other, components of other systems, and their abiotic environment. Adaptation by one system component to any one of these can affect the fitness of other system components.

Figure 4.1 captures the core subject matter of this chapter. It shows the evolution of a system. This term will be specified below. The complex adaptive system comprises components that interact with each other, with other systems and their components, and with the environment. The dynamic nature of these interactions, of the environment of the complex adaptive system and so of selection processes, generates feedback mechanisms that cause the system to evolve. The balance between these two feedback mechanisms determines the extremes in system evolution, indicated by the three alternative states of the evolving system in Figure 4.1. The balance is usually tipped towards negative feedbacks, self-maintenance, and gradual change that build on the existing components and their patterns of interaction. This is indicated by the system on the left.

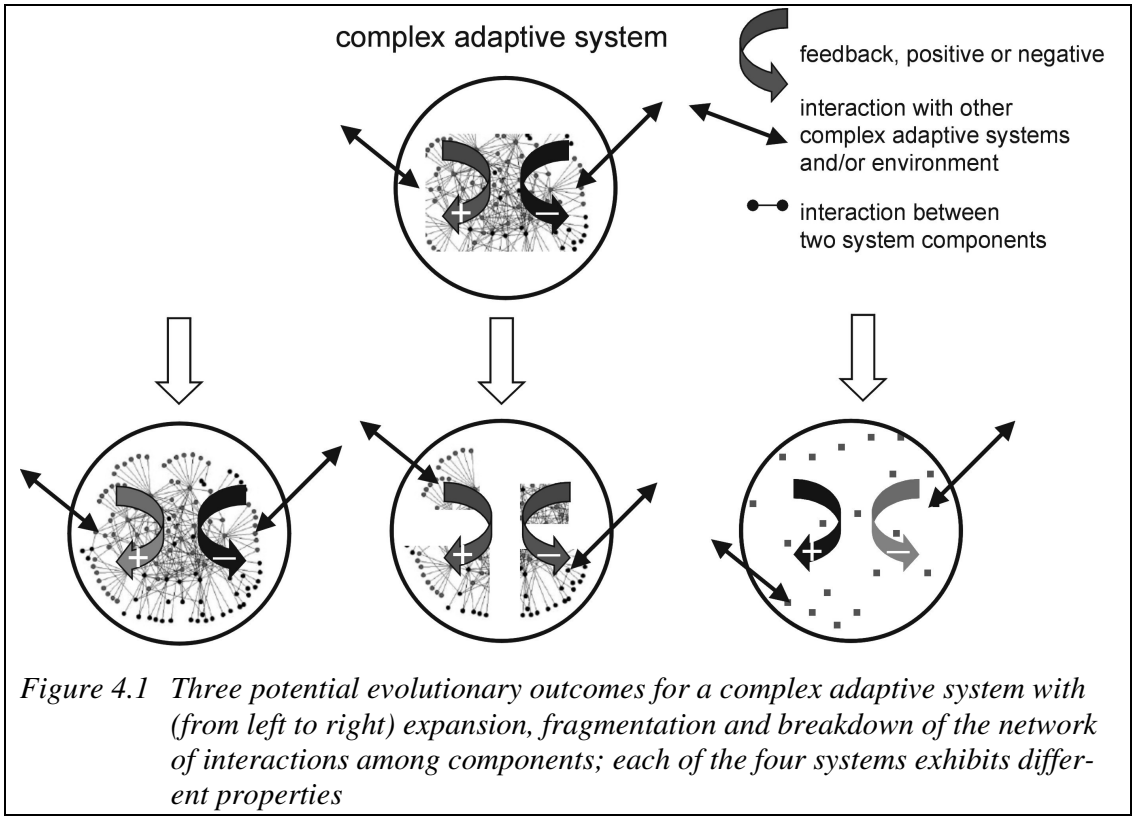


Figure 4.1 Three potential evolutionary outcomes for a complex adaptive system with (from left to right) expansion, fragmentation and breakdown of the network of interactions among components; each of the four systems exhibits different properties

Rare events, or rare combinations of events, can cause feedback balances to tip towards positive feedbacks. The amplifying, rather than dampening, effect of positive feedbacks leads to an abrupt change and partial, or complete, destruction of the system. The web of

interactions fragments and some components may be lost, as indicated by the middle system. Destruction may be so severe that all interactions break down, as indicated by the system on the right, leaving dissociated system components. In both cases, what remain after the positive feedbacks have played themselves out become the building blocks as a new system reorganises.

Evolutionary biologists do not generally accept the notion that systems evolve. They argue that such evolution can be reduced to natural selection operating at the level of the individual. This chapter makes a bridge with the previous chapter by first examining, in Section 4.2, arguments that selection can occur at hierarchical levels other than the individual. Section 4.3 then turns to the study of complex systems where system evolution is a basic tenet. Ecosystems may not be the only biological, complex system. For example, Helighen (1999) considers all levels of the biological hierarchy, from cell to biome, to be complex systems. While the basic principles for the evolution of complex systems are briefly outlined, this section focuses on the 'adaptive cycle', a concept introduced by Crawford (Buz) Holling in his general model of systemic change. It parallels Ilya Prigogine's observation that complex systems can alternate between ordered and disordered or chaotic states (Prigogine 1984; Prigogine & Stengers 1985).

Movement through the adaptive cycle, particularly through the growth and conservation phases, is driven, in part, by coevolution among a system's components. This coevolution is the product of selection for components and interactions that 'fit' well together. Section 4.4 addresses such coevolution. The hierarchical nature of many complex systems, and the tendency for systems to be nested, means that the components of complex systems are complex systems themselves. Consequently the evolution and coevolution of complex systems are closely intertwined.

The main driver behind coevolution is interaction. Section 4.5 returns to this aspect, by reviewing the literature on complex networks. Complex networks capture the pattern and nature of interactions among the components of complex systems. Many complex networks of very different origins have similar topologies, and topology could be related to network robustness. This research is reviewed in Section 4.5.

Robustness is a stability concept (see Chapter 2). As was shown in Chapter 2, ecologists currently think that the pattern, strength and function of interactions among species lie behind ecosystem stability. The study of food webs as complex networks is a focus shared by ecologists as well as those studying complex systems. Section 4.6 reviews this literature. Section 4.7 draws conclusions from my literature review and leads into chapters that develop the theory further.

4.2 Multilevel selection

4.2.1 Introduction

The term 'multilevel selection' is used to encompass a range of terms found in the literature such as group selection (e.g. Sober & Wilson 1998), species selection (e.g. Gould & Lloyd 1999), community selection (e.g. Goodnight 1990a and b), and ecosystem selection (e.g. Swenson *et al*. 2000, Goodnight 2000). Charles Darwin himself proposed that selection could affect groups of organisms (Darwin 1871 p500). If the ingredients of

natural selection – phenotypic variation, fitness, and heritability – exist at the level of groups, then groups can evolve into adaptive units. However in the m id-1960's, this notion became almost anathema to evolutionary biologists who argued that cases of multilevel selection could either be reduced to selection operating at the individual level, or that its effects would be insignificant (e.g. Mayr 1997; Futuyma 1998). Resurgence of interest and research into multilevel selection during the last decade or so has occurred primarily in the fields of socio-biology and evolutionary psychology (Wilson & Sober 1994).

Much, but not all, research on multilevel selection addresses the question of how altruism evolved. Altruism is demonstrated primarily by social species, such as ants and humans, and involves individual sacrifice for group benefit. Altruistic traits decrease the relative fitness of altruists relative to non-altruists. Natural selection at the individual level would favour non-altruists, making the persistence of altruistic traits difficult to explain. However groups of altruists may be fitter than groups of non-altruists. Selection at the group level may facilitate the evolution of an altruistic trait because it confers a fitness advantage to the group over other groups, and because this advantage outweighs the disadvantage to the individual members of the group. Group or multilevel selection may not necessarily favour altruistic traits. However there does seem to be a trend, particularly in social species, towards the moderation of individual striving to survive for the betterment of the group's survival.

A prerequisite for all multilevel selection research is the existence of groups and this implies structure in the distribution of organisms. Laboratory experiments with multilevel selection suggest a second prerequisite: biotic interaction (Goodnight & Stevens 1997). Interaction among individuals within a group can have a bearing on the fitness, not only of the individuals comprising the group, but also of the group as a whole. This interaction may be intraspecific as in a population or family unit. It may also be interspecific if the group comprises multiple species, such as a community or a functional feeding group (or 'guild'). Further, competition would seem to be the major factor determining the reproductive success of the members of a particular group.

4.2.2 Themes within multilevel selection

Multilevel selection is defined as 'variation in the fitness of an individual due to properties of the group or groups of which it is a member' (Stevens *et al*. 1995). For any sort of selection to occur on a phenotype, this phenotype must be heritable and must vary among individuals. The variation must be organised so that there are correlations among members of the group, and variation in the phenotypes of specific individuals must influence the fitness of neighbouring individuals for intergroup selection to occur. Finally there will be a detectable response to selection only if there is among-group genetic variance (Linhart 1999). The significance of multilevel selection in evolution is still unclear. While it appears to have been of minor importance in producing complex adaptations, it seems to be of major importance in determining the many characteristics often grouped under the term 'altruism' (Sober & Wilson 1998). Multilevel selection appears to be particularly relevant in social animals (Wilson & Sober 1994; Sober & Wilson 1998).

Experimental and theoretical studies of multilevel selection trace their origin to the work of Sewall Wright (1968, 1977). Wright envisaged an adaptive landscape, a topography in which natural selection at the individual level leads to peaks of high and troughs of low fitness. Figure 4.2 presents such an adaptive landscape. Natural selection, directed towards the individuals in a population, may be seen as a conservative force that pushes any given population up a single adaptive peak. This effect is moderated by gene flow among populations that serves to level out peaks and troughs and to average fitness over populations and so over the species.

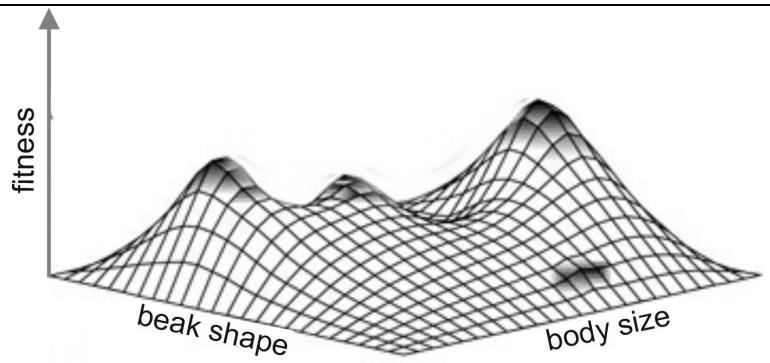


Figure 4.2 Adaptive landscape for a Galapagos finch with regards to two traits, beak shape and body size; peaks (shaded) are regions of highest fitness and valleys are regions of lowest fitness (Grant and Grant 2002)

However Wright also envisaged that many populations are highly structured and dispersed across the landscape in discrete units or groups. The modern term for this is a metapopulation, where a population consists of an assembly of spatially isolated but interacting subpopulations that establish and die out in a dynamic environment. Wright argued that there is competition among subpopulations to survive. Structuring restricts mixing among subpopulations that, in turn, restricts gene flow and facilitates genetic drift. Rather than an averaging of traits, genetic differences among subpopulations are maintained and some subpopulations will come to occupy peaks on the species' adaptive landscape. Their greater fitness means a greater chance of survival, and the likelihood that they will replace (out-compete) subpopulations occupying lower adaptive positions. Species existing in structured populations may then be able to achieve a greater fitness than those in unstructured populations.

According to Goodnight & Stevens (1997) there are two themes within multilevel selection research. Much of the controversy and debate has occurred around the theme of altruism. While multilevel selection does not have to involve altruism, altruistic traits appear to be favoured by this form of selection. Research within the altruism theme focuses on observing existing phenotypes such as adaptive behaviours and hypothesizing plausible evolutionary mechanisms for their existence. Many potential evolutionary pathways for a particular trait exist. Some pathways involve within-group selection (i.e. individual or natural selection), whereas others may involve between-group selection, or even selection acting simultaneously at multiple levels (multilevel selection). The most plausible pathway from all possible pathways is then sought, and this requires the development of rules for deciding which are more likely.

The second theme addresses the concept of groups as adaptive units and is experimentally oriented. Research attempts to resolve some of the major controversies about between-group selection, provide insight into the importance of between-group selection in natural populations, and suggest novel evolutionary consequences of multilevel selection. An example of this research is provided in Box 4.1.

Box 4.1 Selection for egg production in hens (Craig & Muir 1996, Muir, 1996 in Goodnight & Stevat ens 1997)

The advent of 'egg factories' has resulted in housing hens as groups in cages rather than the more traditional open pens. The efficiency of maintaining a large number of hens is improved, but the hens become aggressive in the small cages. This increases mortality and reduces egg production. Individual selection for high productivity results in a negative response when individuals are placed together.

Craig and Muir applied between-group selection, selecting cages rather than individuals for high egg production. In contrast to the above response, they observed a 160% increase in annual egg production per hen compared with that for unselected controls. The selected line also showed fewer aggressive interactions and lower mortality. Aggressive interactions decreased to the extent that beak trimming was not required; mortality decreased 29%.

There are some 250 million laying hens in the USA. Eliminating beak trimming at 5 cents per bird and reducing mortality of birds worth $3.50 each could yield savings thexceed the birds' appraised value of about US$3 million.

Multilevel selection has been demonstrated for groups within populations (red flour beetle *Tribolium castaneum*, domestic rat *Rattus rattus*, the plant *Arabidopsis thaliana*, and hens – various references in Goodnight & Stevens (1997), within two-species communities (*Tribolium castaneum* and *T. confusum* – various references in Goodnight & Stevens 1997) and small ecosystems (soil microcosms and aquatic microcosms – Swenson *et al*. 2000). Goodnight and Stevens also reviewed five studies conducted on naturally occurring species. They hypothesise that multilevel selection may eventually explain many commonly accepted processes, such as kin selection and frequency-dependent selection, which cannot be adequately explained by within-group selection.

4.2.3 Summary

Evolutionary biology offers mechanisms to explain the evolution of species in terms of genes within individuals forming populations. It is argued that evolution at higher levels, of groups such as populations, communities and ecosystems, can be reduced to this fundamental mechanism. However multilevel selection argues that groups of individuals may be selected over other individuals and other groups of individuals. It offers the persistence of 'altruistic' traits, in the broadest possible sense, as evidence of such selection. It also offers laboratory experiments that clearly demonstrate that multilevel selection can occur. The object of selection is essentially the same – the gene – but the vehicle of selection, or mechanism by which genes convey fitness, is at a level higher than the individual. Fitness becomes more than an individual's ability to contribute to subsequent generations as the persistence of a group will also enhance the survival of its component individuals.

Multilevel selection is controversial within evolutionary biology. It would seem clear that it occurs but, as emphasised by Mayr (1997), it is not clear how commonly it occurs, nor how significant its effects are. Some authors allow the possibility that it may be involved in macroevolutionary processes (e.g. Ridley 1996 when discussing species selection). The difference between microevolution and macroevolution may be illustrated by comparing the (micro)evolution of greater speed in rabbits to escape foxes, with the (macro)evolution of wings so that birds could fly. Macroevolution is poorly understood, and does not seem to be explainable in terms of microevolutionary processes only.

One arena where multilevel selection is uncontroversial is in the study of complex systems. Here all complex systems, whether comprised of individual organisms or, say, firms or family units, are capable of evolving. The notion of coevolution among these system components draws heavily on Wright's adaptive landscape.

4.3 The evolution of complex systems

4.3.1 Introducing complexity

Complex systems' thinking follows in the tradition of von Bertalanffy's general systems theory (Bertalanffy 1968; Bertalanffy 1975). It also draws on other concepts that have emerged in recent decades such as catastrophe, chaos and complexity theory, non-equilibrium thermodynamics and self-organisation, and Jaynesian information theory (Kay *et al*. 1999). The study of complex systems began with the work of Ilya Prigogine (Prigogine 1984), a physicist who was bothered by the contradiction between the Second Law of thermodynamics and biological evolution. The Second Law of Thermodynamics holds that the universe is moving toward increasing entropy, or 'running down', yet biological evolution demonstrates that increasing order and structure mark at least part of the universe. Prigogine understood that systems could run down but that another option was available, particularly to open systems with their access to external sources of energy. Such systems could re-constitute at a higher level of complexity. According to Prigogine, systems of all sorts follow a path that begins in order, passes through chaos, and then may end, not just in new order, but in a vastly improved new order.

While Prigogine was exploring the growth of order in 'dissipative structures' in the physical world, Stuart Kauffman, John Holland, and others at the Santa Fe Institute were working to understand the processes of evolutionary change and self-organisation in the organic world, clearly the most obvious dissipative structure in nature. Kauffman (1995) set himself the considerable task of determining the means whereby life progressed from primordial molecular stew to the organisms and their ecosystems that are around today. Through extensive computer modelling, real life laboratory work, and a combination of both, Kauffman came to the conclusion that, given a few very simple pre-conditions, systems will self-organize. A crucial element of the self-organising potential of a system is a high degree of complexity, which should exceed a critical threshold. The term for the resulting self-organized system is 'complex adaptive system' (see also Holland 1995). Evolution and coevolution are characteristics of complex adaptive systems.

This section treats the issue of complex systems and complex adaptive systems selectively. The focus is on concepts that elucidate how such systems evolve. The study of

complex systems is a relatively new (trans)discipline and, as with other disciplines, has developed its own terminology and language that may be impenetrable to non-initiates. Garcia (1999) provides a detailed and structured presentation of the various complexity concepts, which summarised in Table 4.1.

Table 4.1 Complexity concepts in the study of complex adaptive systems (Garcia 1999)

Self-organisation	**Evolution**
Emergence Complex adaptive systems consist of processes of mutual adjustment and self-regulation rather than of central direction. Out of the interactions of the independent agents in a system, an overall pattern, structure or organisation emerges that it is not simply an aggregation of individual actions, but has unique properties not possessed by the individuals alone. *Hierarchy* Complex systems have no single vertical control structure but rather have stratified autonomy, with hierarchically nested processes linking micro and macro levels in a loosely coupled manner. *Self-similarity* Self-similarity means that features of a structure or process look alike at different scales of space or time. Chaotic systems show self-similarity across time scales; fractal objects show self-similarity across spatial scales. *Feedback* In ecological systems, positive feedback in the form of destabilising forces maintains diversity, resilience and opportunity for novelty, while negative feedback maintains productivity and biogeochemical cycling. *Attractors* The interplay of feedback processes generates macro patterns termed bounded stability. These patterns are similar to the chaotic or strange attractors of chaos theory. 'Order out of chaos' provides an image of macro-level pattern emerging out of micro-level randomness.	*Bifurcation* Bifurcations in a complex adaptive system are abrupt and dramatic qualitative changes in system behaviour pattern as a result of small, endogenously-caused changes in parameter values. *Sensitivity* Sensitivity embodies the idea that complex systems are fundamentally non-linear in causation and can generate unpredictable outcomes across space and in time. *Criticality* Self-organised criticality argues that the distribution of fluctuations in complex systems, from many small to a few large, is no coincidence. Although a system in a critical state can trigger cascades of all magnitudes, a system exhibits complex behaviour only if it has just the right balance of stability and fluidity. *Path dependence* Complex adaptive systems typically possess a multiplicity of potentially stable states, but the one which emerges depends on the system's 'small event history' – the sequencing and cumulation of random events, actions and conditions. Any outcome is dependent on the historical path taken to it. *Coevolution* Agents occupy a dynamic environment produced by its interactions with other agents. Mutual or reciprocal causality – fields of relations that are mutually determining and determined – leads to reciprocal adaptation.

It is worth noting that different authors emphasise different concepts. For example, Holling's adaptive cycle (Holling 1986) emphasises self-similarity, as the cycle appears to occur within each nested level of ecological systems, ranging from scales of hours and centimetres to those of millennia and thousands of kilometres (Garcia 1999). One of the most widely cited theories in complexity science is self-organised criticality (SOC), de-

veloped by Per Bak and associates (Bak *et al*. 1988; Bak 1996). SOC emphasises that the effects of a constant-size perturbation vary from small to large according to a power-law (see also Box 4.2). James Kay also addresses self-organised criticality within SOHO (self-organising holarchic open) systems. In providing a management context, he and his co-authors emphasise that decision-makers have the task of choosing among attractors. Management involves promoting feedback processes that yield the desired attractor and discouraging feedback processes that yield undesired attractors (Kay *et al*. 1999).

Box 4.2 Power laws, fractals and self-organised criticality

Relations of the form:

$$y = kx^h$$

are called power-law relations. Science is filled with power laws, for example:

- Newton's law of gravitation, the relation between the gravitational force (F) between two objects and their distance (r): $F = GMmr^{-2}$; and
- allometry of animal metabolic rates: metabolic rate $= k(weight)^{3/4}$.

A fractal, or fractional power law, involves a power-law relationship where h is not a natural number but a fraction. The rationale for the wide applicability of fractals is that fractional power laws are the only statistical distribution that is scale invariant (Limburg *et al*. 2002). Fractals have been used as scalars to describe such complex structures as cloud shape, river drainage patterns, coastline lengths, lung surface areas and landscape patches.

Per Bak's theory of self-organised criticality (Bak *et al*. 1988; Bak 1996) argues that large interactive systems naturally evolve toward a self-organised critical state in which a minor event can lead to a cascade of events.

Consider a tabletop onto which sand is dropped at a uniform rate. The sand piles up and begins to slide off the edges of the table. Eventually the system reaches a steady state at which the mean rate of sand dropping onto the pile equals the mean rate at which sand falls over the edges. Assume that a single grain of sand is added to the pile at a random location, triggering an avalanche. Bak *et al*. find a power-law distribution relating avalanche frequencies and sizes, with many tiny and a few large ones. The system under investigation has attained and maintained a kind of poised state able to propagate perturbations or avalanches on all possible length or size scales. When a system is at such a self-organised critical state, the frequency and magnitude of events follow a power-law distribution. This may be viewed as a statistically stable, internally controlled state with no characteristic scale within the system. At this point, events are correlated across all scales exhibiting a statistical fractal pattern in spatial structure (Wu & David 2002).

4.3.2 Complex systems and complex adaptive systems

The term 'complexity' has become a buzzword across many scientific fields (Gell-Mann 1995; Edmonds 1999; Wu & Marceau 2002). Many disciplines are involved in investigating complexity and this poses challenges for a mutually acceptable yet precise definition. The point about complexity is that it cannot be ‘reduced’ into separate, component parts for analysis. Crucial information or characteristics are lost with such a reductionist approach. Helighen (1999) emphasises a duality, in that the components of complex systems are simultaneously distinct yet connected. Complexity may have different facets, as illustrated by three examples (Wu & Marceau 2002):

1. structural complexity, which may refer to the compositional diversity and configurational intricacy of a system;

2. functional complexity, which emphasises the heterogeneity and non-linearity in system dynamics; and,
3. self-organising complexity, which hinges on the emergent properties of systems co-evolving with their environment primarily through local interactions and feedbacks at different spatiotemporal scales.

Distinction and connection are the two central features of complexity (Helighen 1999). Distinction implies variety and differentiation, which in turn lead to disorder. Connection implies constraint and integration, leading to order. Complexity exists if processes creating both distinction and connection are present and the result is something intermediate between perfect disorder and perfect order. Processes generating order involve negative or dampening feedbacks; processes generating disorder involve positive or amplifying feedbacks. Many, if not most, complex systems are 'on the edge of chaos' (Waldrop 1992); they are in a locally stable equilibrium, or are metastable, and can undergo rapid transitions to a new equilibrium state (e.g. Peterson 2003; Limburg *et al*. 2002).

The perception of complexity depends on the scale of observation, so that what is complex in one representation may be ordered or disordered in another. Helighen (1999) illustrates this by considering the complex pattern of cracks in dried mud. Looking at the mud plain from a distance, the cracks disappear and the surface may appear flat and homogeneous. At the scale of the different clay particles forming the mud, it may be a completely disordered array. The pattern of crack structure is apparent only at an intermediate scale. A system with distinguishable structure over a few scales is termed 'scale-thin'. In contrast, fractals or self-similar shapes have an infinite scale extension. At every scale of observation, new details are revealed, yet these details are reminiscent of details elsewhere in the fractal object or in the same part of the object, but on a different scale. Such systems are variously termed 'scale-free', 'scale independent', or 'scale invariant'.

Complex systems share several common characteristics (Wu & Marceau 2002): they are thermodynamically open in that they exchange energy and/or mass with their environment; they are often composed of a large number of diverse components; system components interact with each other nonlinearly and frequently have response delays and feedback loops among them; and complex systems exhibit a high degree of heterogeneity in both time and space. Consequently, complex systems are often characterized by emergent properties, multiscale interactions, unexpected behaviours, and self-organization. Complex systems include various biological, physical, technological and social systems and comprise two broad groups. Complex deterministic, or non-adaptive, systems have constant parameters that define the behaviour of the system. Chaos theory focuses on such systems that are, for the most part, physical and comprise inanimate components. In contrast, complex adaptive systems comprise animate 'agents'.

A complex adaptive system is capable of self-organisation. The term was defined by Levin (1999 in Wu & Marceau 2002, p1) as: "a system composed of a heterogeneous assemblage of types, in which structure and functioning emerge from the balance between the constant production of diversity, due to various forces, and the winnowing of that diversity through a selection process mediated by local interactions". Most ecological and social systems exhibit self-organising complexity and are considered to be complex adaptive systems. Positive and negative feedback processes operating over a range of spatial and temporal scales dominate the dynamics of these systems.

Complex adaptive systems share a number of features (e.g. Kauffman 1995; Garcia 1999) that may be summarised as:

- complex adaptive systems consist of a network of many agents acting in a self-managed manner and without centralised control of their actions;
- agents exist in an environment characterised by interactions, with each other and with their physical surroundings, are constantly acting and reacting to what other agents are doing, and so cause their environment to change, to evolve and to generate perpetual novelty;
- organised patterns of behaviour arise from interactions among agents, producing 'wholes' whose specific structures arise from the distinction and interdependency of their parts;
- agents are constantly organising and reorganising themselves into larger structures having many levels of organisation, with agents at one level serving as building blocks for agents at a higher level;
- there are specialised niches occupied by agents adapted to exploit them, dynamics as old niches disappear and new ones are created in response to environmental changes, and the filling or loss of new niches often leading to the creation or loss of additional niches – speciation and extinction are not only driven by endogenous processes, but they also may indicate the cascading effects of a positive feedback;
- agents can anticipate the future, to varying degrees, or make 'predictions' based on internal models; and,
- agents coevolve.

4.3.3 The evolution of complex systems

In trying to span disciplines to explain observations and concepts, the literature from complex systems is often imprecise and inconsistent in its language. The term evolution may be used in specifically defined contexts, or it may be used in a colloquial sense where it encompasses virtually all sources of change. The latter may be attributed to the 'popularity' of complex systems thinking, to its penetration into various disciplines, and, perhaps consequently, to misunderstanding and misuse of terms.

Some authors attempt to describe complex systems' evolution in terms of biological evolution in an attempt to reconcile the two, or at least to highlight differences (e.g. Nelson 1995; Garcia 1999; Bergh 2005; Hodgson 2002). Others argue for self-organisation as a new, overarching paradigm to explain all kinds of evolution (e.g. Witt 1997 and Foster 1997 but countered by Hodgson 2002). It is not yet clear whether complex systems' evolution is fundamentally different from biological evolution, whether biological evolution is a subset of more general processes such as self-organisation, or whether the behaviour of complex systems is being forced into an existing framework of understanding.

My concern lies with the last, and leads to my second criticism. There is an imbalance in the literature between the development of concepts explaining the evolution of complex systems and their empirical validation. Greater precision in language may be found in publications modelling complex systems mathematically. Because my focus is more conceptual than mathematical, I have consulted only a limited selection of these publica-

tions. However those consulted exhibited neither a strong empirical basis nor anything beyond superficial corroboration from real world systems.

A variety of factors, both endogenous and exogenous, can effect changes to complex systems. Different types of change are often not well distinguished, and this gives the impression that virtually all change effected to complex systems may be considered evolutionary change. Many authors point to the interplay between positive and negative feedbacks when explaining evolution – positive feedbacks generate variety on which negative feedbacks winnow (e.g. Nelson 1995; Helighen 1999; Bergh 2005; Winder *et al*. 2005). They draw parallels between this interplay and the process of natural selection. These discussions implicitly equate a complex system with a population of a species. The components of both, agents in the former and individuals in the latter, display a variety of phenotypes expressed in terms of physical characteristics such as size or colour, as well as behaviour and learning capacity. Selective processes promote the survival of agents with phenotypes that fit best with other system components, are better suited to the environment of the complex system, and support the complex system itself in its struggle to endure as an agent within some higher order complex system. In parallel with evolutionary biology, the evolution of complex systems is seen to revolve around the achievement of greater fitness. Helighen (1999 p24) defines this fitness as "an assumed property of a system that determines the probability that that system will be selected, i.e. that it will survive, reproduce or be produced".

While there are various perspectives on the evolution of complex systems, and most studies of complex systems are addressing their evolution in some way, I have confined my discussion to the adaptive cycle. The adaptive cycle describes the path followed by complex adaptive systems, as they begin in order, pass through chaos, and emerge in new order. It describes for complex adaptive systems what Ilya Prigogine observed for complex deterministic systems. Use of 'adaptive' has evolutionary implications but does not conform to evolutionary biological definitions. The components of complex adaptive systems display adjustments, or adaptive responses, to their dynamic and changing environment. Adaptive responses are partly responsible for moving systems through the various phases of the cycle.

4.3.4 The adaptive cycle

The adaptive cycle provides a conceptual representation of the dynamics of complex adaptive systems. It was first proposed by Holling (1986) in his general model of systemic change but has been further refined in, for example, Gunderson *et al*. (1995), Peterson (2003) and Kay *et al*. (1999). The adaptive cycle proposes that the internal dynamics of systems cycle through four phases as indicated in Figure 4.3: rapid growth (r), conservation (K), release (Ω), and reorganisation (α). Kay *et al*. (1999) interpreted the adaptive cycle from the perspective of self-organisation based on thermodynamics.

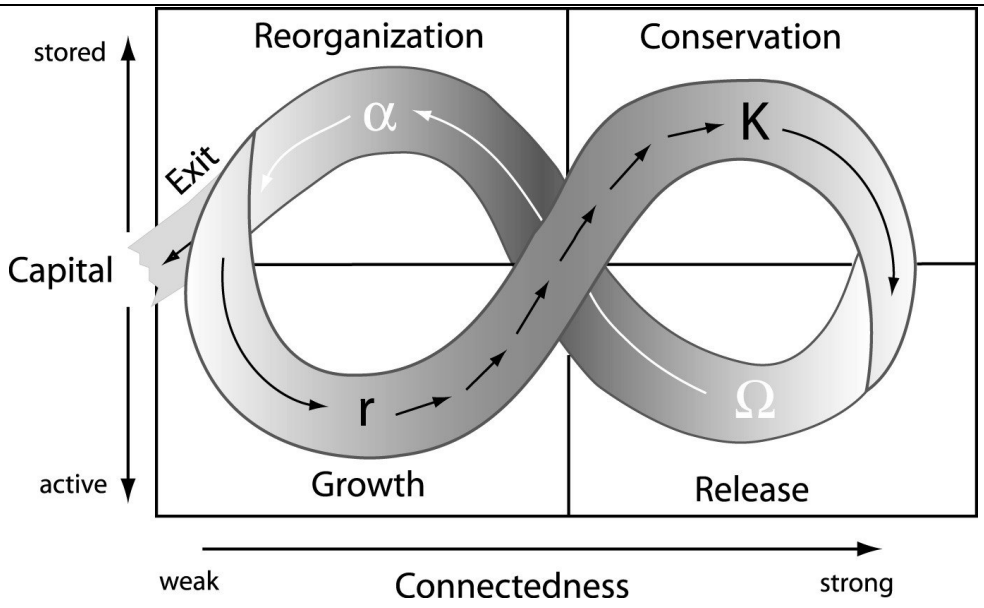


Figure 4.3 The adaptive cycle (redrawn from Peterson 2003)

The rate at which a system moves from one phase to another is indicated in Figure 4.3 by the arrows: short, closely spaced arrows indicated slow and predictable change while long arrows indicate rapid and less predictable change. The following elaboration draws from Peterson (2003) and from Kay *et al*. (1999) and addresses ecological systems. Examples of each phase, for both ecosystems and social systems, are offered in Box 4.3.

Box 4.3 Examples of systems from each of the four phases of the adaptive cycle (Peterson 2003)

Growth (r)

Ecosystems: vegetative control of microclimate
Social systems: bureaucratic rationalisation

Conservation (K)

Ecosystems: an old-growth forest
Social systems: a large corporation, such as Microsoft, that comes close to monopolising its markets.

Release (Ω)

Ecosystems: fire, insect outbreaks, floods, disease outbreaks, equilibrium shifts
Social systems: financial panics, banking crises, revolutions, pollution events.

Reorganisation(α)

Ecosystems: emerging state after an equilibrium shift, such as algal-dominated freshwater lakes with turbid water replacing macrophyte-dominated lakes with clear water following human-induced eutrophication (e.g. Scheffer & Beets 1994; Hosper 1997).
Social systems: the radically different structure of Eastern European countries following the collapse of the Soviet Union.

Kay *et al*. (1999) characterise the adaptive cycle as being characterised by two thermodynamic branches or self-organising pathways. The first, growth (*r*) to conservation (*K*) is driven by the exergy – that part of energy capable of being transformed into work – in solar energy and results in increasing biomass. The system grows, accumulates resources and stores exergy. Initially the system's components are weakly connected to one an-

other and its internal state is weakly regulated. The components that thrive are those that develop interrelationships reducing the impacts of external variation and reinforcing their own expansion. As the system approaches the *K* phase, it becomes more organized. Competitive advantage shifts from agents that are able to grow rapidly despite environmental variation to those that can effectively manage and benefit from intense competitive and cooperative interactions with other agents. Increased system connectivity and efficient resource use leave few opportunities available for new agents to enter the system. The future dynamics of a system in this state appear to be gradual, constrained, predictable, and dominated by negative feedback processes.

The *r* and *K* phases lead to a paradox. The system has increased its effectiveness in consuming exergy, has become more organised to do so, and it contains more exergy. This, in turn, increases its vulnerability should other self-organising, dissipative processes, such as fire, outbreaks of pests or disease, take advantage of this stored exergy. In thermodynamic terms, the *K* phase represents a point of maximum thermodynamic organisation – the system is using the available exergy as fully as possible. It also represents a point of maximum thermodynamic risk as it is as far out of thermodynamic equilibrium as possible. In the *K* phase, a system is balanced between the two main attractors of complex systems – local thermodynamic equilibrium and maximum exergy consumption. For some systems this balance is precarious, for others less so, suggesting various degrees of being 'on the edge of chaos'. In the end the local equilibrium attractor is always dominant and the system eventually moves into the second thermodynamic branch.

The second thermodynamic branch, release (Ω) to reorganisation (α), releases exergy and nutrients. Relative to the first branch, systems move through this branch very quickly. A self-organising process unfolds in the direction of increasing exergy consumption but the processes are fundamentally different from those in the first branch. Instead of storing biomass and exergy, the nutrients and exergy already stored in biomass are released. Release is triggered by a perturbation that exceeds a system's resilience and succeeds in breaking apart the web of negative feedbacks maintaining it. The system flips abruptly into a transitory disturbance state that rapidly disperses the system's accumulated capital and connections until the disturbance exhausts itself. Raw materials are now available to reorganise and then begin the cycle again, but the system's boundaries and internal connections are tenuous. Such a loosely defined system can easily lose or gain resources and agents, can be reorganized by small inputs, and can be shaped by chance events. The lack of systemic connection and control makes it difficult to predict what type of organization will form. Which specific path is followed is a function of the biological information and nutrients available, and environmental conditions at the time.

The direction of both thermodynamic branches is towards increased exergy consumption. A complex adaptive system, such as an ecosystem, alternates between these two qualitatively different pathways of self-organisation that comprise the adaptive cycle. The first branch has been traditionally referred to as succession or ecosystem development. The second branch is analogous to Schumpeter's creative destruction (Schumpeter 1964 in Peterson 2003).

Ecologists are devoting much attention to abrupt changes in ecosystems (e.g. Scheffer & Carpenter 2003; Rietkerk *et al*. 2004; Nes & Scheffer 2005). Scheffer and Carpenter highlight that stable states are really dynamic regimes. Ecosystems are always changing,

if only slowly. Although intrinsically-generated dynamics and the effect of external forces are difficult to unravel, 'fluctuation' rather than 'stable state' appears to be the rule. Many authors argue for the use of 'regimes' instead of terms such as 'stable states' or 'equilibria' that seem to exclude dynamics (see also Carpenter 2003). The term 'regime shift', also used in oceanography (e.g. Francis & Hare 1994; Collie *et al*. 2004), describes sudden shifts in ecosystems. A regime shift may be defined as a rapid reorganization of ecosystems from one relatively stable state to another (e.g. Rodionov & Overland 2005). This term will be encountered in subsequent chapters. A regime shift may be the outcome of the second thermodynamic branch of the adaptive cycle.

4.4 The coevolution of systems

4.4.1 A reconciliation

The evolution of complex systems is viewed in terms of the interplay between positive and negative feedbacks. While parallels may be draws with biological evolution, those studying complex systems generally admit that the classic evolutionary model is difficult to reconcile with a systems-oriented model. Garcia (1999) suggests that the addition of a step to the classic model would serve reconciliation. The extra step draws on the adaptive cycle outlined above, and emphasises the system-wide effects that evolutionary change by a component may cause. Such evolutionary change has two basic effects.

The first is 'readjustment'. The selective retention of a new phenotype has fitness implications for other interlinked system components and may lead to changes in the mix of phenotypes comprising the system. Such readjustment occurs primarily during the *r* and *K* phases of the adaptive cycle, as system components and phenotypes are selected according to their ability to accumulate resources, store exergy and build on interrelationships with other system components. The building on interrelation ships implies coevolution. Readjustment involves system-wide changes that are very small, with a predominance of negative feedback mechanisms geared to maintain the status quo.

If readjustment exceeds a threshold, a cascade of effects may be triggered that leads to the second effect, which is system 'destruction'. The system is assumed to be located at a level of self-organised criticality or in the *K* phase of the adaptive cycle where its resilience is low and its vulnerability is high (Peterson 2003). The majority of new phenotypic variations have died out due to the predominance of negative feedback mechanisms. Adjustment, perhaps in conjunction with a unique confluence of small events, triggers positive feedbacks and so causes a large evolutionary impact. The system flips from the *K* to the Ω phase, followed by reorganisation (α) and a new cycle.

A management perspective based on this view confines the focus to systems located in the first thermodynamic branch of the adaptive cycle. System change here progresses slowly and so is potentially amenable to manipulation. The flip from *K* to Ω is abrupt. Subsequent management efforts, if they can be so named, are urgent and likely to be directed more towards short term concerns such as damage control. During the growth and conservation phases, management can be more strategic and take a view that encompasses the medium and long term. Management objectives vary, but I would argue that they are frequently conservative and risk averse. We are uncertain whether an abrupt flip

into release by the current social system, or by the natural systems on which we depend, would lead to a new system that provides the goods and services we currently value.

Kay *et al*. (1999) argued that management involves promoting feedback processes that yield the desired attractor, and discouraging feedback processes that yield undesired attractors. Combined with a risk-averse attitude, management devolves into two broad goals: management of readjustment so that it does not exceed thresholds; and, maintaining the system without jeopardising its resilience. The management of readjustment implies the management of coevolution, described by Garcia (1999 p294) as follows:

> *"In complex adaptive systems, each agent finds itself in a dynamic 'environment' produced by its interactions with other agents. Agents are constantly acting and reacting to what other agents are doing, engaging in a fluctuating interplay of cooperation and competition. The set of strategies available to each agent can be envisioned as a ….. landscape of 'fitness' ……. Each agent has its own fitness landscape but, due to mutual causality, these landscapes are interdependent. As each agent constantly tries to adapt to all the others by moving around on its own fitness landscape, it dynamically changes the landscapes of all the other agents as well ….. Mutual causality leads to mutual adaptation"*.

4.4.2 Coupled dancing landscapes

Stuart Kauffman (1993, 1995) pioneered the notion of coevolution and developed models to elaborate it. Kauffman's view of coevolution parallels evolutionary biology, is strongly founded in the biological sciences, yet is not strict reciprocal adaptation as discussed in Chapter 3. The introductory sentence to Kauffman's chapter on the dynamics of coevolving systems frames his view (Kauffman 1993 p237):

> *"The true and stunning success of biology reflects the fact that organisms do not merely evolve, they* coevolve *both with other organisms and with a changing abiotic environment"*.

Kauffman's concept of coevolution emphasises the myriad interactions and reciprocal influences among organisms sharing a given environment. There is also a fundamental difference between simple adaptive evolution and coevolution. Evolution on a fixed fitness landscape, as illustrated in Figure 4.2, pushes species towards local optima that are single points. In a coevolutionary process, the fitness landscape for any system component is not fixed. It heaves and deforms as other system components make their own adaptive moves. This image of a dynamic jockeying for position among interacting components of a complex adaptive system is central to coevolution within complex systems.

The adaptive landscapes of agents within a complex system, such as species in an ecosystem or firms in an economy, are coupled. Independent adaptive moves by agents to increase their fitness affect the fitness of other agents. Stuart Kauffman (1993) coined the term 'coupled dancing landscapes' to capture these interdependencies among the components of a complex system. The deformation of adaptive landscapes can be so drastic that none of the agents can assemble complex integrated properties. Coevolution then becomes an unceasing evolutionary process in which a system continues to change merely to maintain fitness relative to the system with which it coevolves. Many authors refer to this as the Red Queen hypothesis; I termed this escalation in Chapter 3.

In contrast to escalation, Kauffman uses John Maynard Smith's idea of Evolutionary Stable Strategies (ESS). An ESS is achieved when a phenotype emerges such that any other phenotype would result in lower fitness; species may stop evolving once an ESS is attained. Kauffman developed models of coevolution based on the '*NK*' model of fitness landscapes. The models were based on four key parameters: the number, *N*, of traits in a species that depend epistatically on *K* other traits of that species as well as on *C* traits in another species, in a system of *S* species. The results of his models show a number of patterns, two of which are highlighted. Firstly, coevolving model systems can behave in an ordered regime analogous to an evolutionary stable strategy, or in a Red Queen regime. Kauffman demonstrated that a phase transition between order and chaos exists, and that the highest mean fitness occurred at the phase transition.

Secondly, Kauffman examined situations in which the adapting agents could increase or decrease the ruggedness of their own fitness landscapes and could invade one another's niches. Three conclusions from this work are highlighted. Firstly, the agents, each adapting for their own selfish advantage, tuned the ruggedness of their fitness landscapes to an intermediate level, demonstrating that selection could alter the structure of fitness landscapes in this model world. A fitness landscape is not simply imposed on an agent by its environment. Secondly, a 'self-organized critical', poised state emerged with a power-law distribution of speciation and extinction events propagating across the model ecosystem. Thirdly, mean fitness increased and the mean probability of extinction decreased. This raises questions as to whether fitness can be optimised and extinction minimised, and what the mechanisms behind this could be.

Kauffman offered the following hypothesis (p261 – see also Chapter 1):

> *"In coevolution, organisms adapt under natural selection via a* metadynamics *where each organism myopically alters the structure of its fitness landscape and the extent to which that landscape is deformed by the adaptive moves of other organisms, such that…. the entire ecosystem coevolves to a poised state at the edge of chaos."*

Myopia refers to organisms' responses that affect only the local properties of the landscape and highlights that an organism cannot overview the whole landscape. Kauffman argues that his results indicate the existence of an attractor, mutually constructed by selfishly optimizing agents, and the existence of small and large, endogenously-driven, avalanches of speciation and extinction events in ecosystems.

There is now quite a literature on modelling efforts to capture coevolution in a wide range of complex systems, for example: artificial neural networks or multi-objective cooperative networks (García-Pedrajas *et al*. 2002); export-led economic growth (Fiorillo 2001); biological systems (Stauffer & Jan 1994; Caldarelli *et al*. 1998; Oliveira *et al*. 2000; Archetti 2000); public relations theory (Murphy 2000); information theory (Wallace & Wallace 1998); the rings of Uranus (Mosqueira *et al*. 1999); technology and industrial capacity (David & Rothwell 1996); game theory (Lindgren & Nordahl 1994; Miller 1996); and, sustainable development (Svirezhev & Svirejeva-Hopkins 1998). The focus in this dissertation is on coevolution as a concept, and less on the specifics of how it could be modelled. Consequently neither this literature nor efforts to model coevolution, are discussed further.

4.4.3 A perspective on coevolution

My view of coevolution draws on the adaptive cycle's representation of system evolution, Garcia's reconciliation of classic evolution with the adaptive cycle, and Kauffman's modelling of coevolution. Garcia and Kauffman highlight the role of coevolution within system evolution. I particularly emphasise the myopic nature of coevolution, that system components effect primarily local changes to adaptive landscapes. Garcia terms this readjustment, with the predominance of negative feedback mechanisms unaffected.

Large evolutionary shifts and unique combinations of small events can lead to system destruction. Positive feedback mechanisms come into play and the system tips over the edge into chaos. Less dramatically, the system flips from the first thermodynamic branch of the adaptive cycle to the second, and may reorganise into a different system. Human actions can cause such regime shifts, as illustrated by freshwater lakes subject to nutrient loading (Scheffer & Beets 1994; Hosper 1997).

The method developed in subsequent chapters draws on this view. I envisage a natural system with a social system dependent on its products. Human intervention in the ecosystem could trigger an evolutionary shift that leads to readjustment, but could also cause system destruction and a regime shift. The extinction of system components with failure to adapt to changing circumstances also comprises one aspect of such a system's evolution. The adaptive cycle highlights that system destruction is preceded by a breakdown of connectedness among system components. A regime shift occurs when a different attractor drives subsequent reorganisation of surviving components and is a clear indication that the course of coevolution has been substantially altered.

4.5 Real world networks

4.5.1 Introduction and context

Interaction is a key theme in this dissertation and is a major focus for those studying complex systems. Disordered networks are receiving much attention as models describing the interactions among components of complex systems (Watts & Strogatz 1998; Watts 1999 in Amaral *et al*. 2000; Barthélémy & Amaral 1999; Barabási & Albert 1999; Albert *et al*. 2000; Lago-Fernandez *et al*. 2000; Callaway *et al*. 2000; Newman 2000). Networks may be represented in various ways but they always comprise nodes or vertices representing the system components and links representing the interactions. Nodes may be poorly connected and interacting with only a few nodes, or highly connected and interacting with many nodes. The latter are also termed hubs.

Any given real world network is the product of past coevolution among components, and captures one state within the evolution of a system as a whole. Parts of the network may be evolutionarily stable while other parts are 'dancing' (see Section 4.4). Even so, it is reasonable to assume that a network constructed from observations of a complex system is a representation of a metastable system. Its stability is bounded and these bounds are unspecified, but it reasonable to assume that those collecting the data to build the network would have been aware of changes in system parameters that would occur with a shift from one stability domain to another. The network is but a snapshot of the metastable system.

4.5.2 From regular lattices and random graphs to small-world

A wide range of disordered or 'real world' networks have been studied including: chemical-reaction networks (Alon *et al*. 1999), neuronal networks (Watts 1999 in Amaral *et al*. 2000), genomic metabolic networks (Tong *et al*. 2004; Ravasz *et al*. 2002), food webs (Pimm & Lawton 1980; Paine 1992; McCann *et al*. 1998; Solé and Montoya 2001; Dunne *et al*. 2002a and b), social networks (Wasserman and Faust 1994; Axtell & Epstein 1999 in Amaral *et al*. 2000), scientific-collaboration networks (Raan 1990), and computer networks (Adamic 1999; Huberman *et al*. 1999; Huberman and Adamic 1999; Adamic *et al*. 2000; Albert *et al*. 2000). Disordered or real world networks are neither regular lattices nor random graphs yet their modelling often assumes such a connection topology (Watts & Strogatz 1998). Regular lattices comprise nodes connected to other nodes according to a specific pattern, such as the molecules in a crystal. Random graphs, at the other extreme, comprise nodes randomly connected to other nodes. Neither of these extremes seems to be an adequate framework within which to study complex systems (Kochen 1989 in Amaral *et al*. 2000). Watts and Strogatz (1998) pioneered research into real world networks by introducing randomness to a regular lattice (see Figure 4.4).

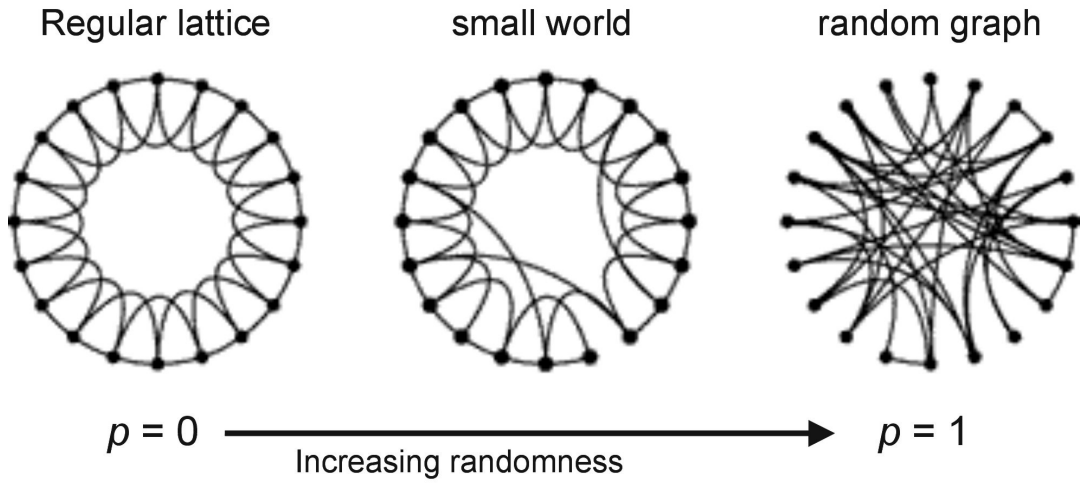


Figure 4.4 From regular lattices, through disordered or small-world networks, to random graphs (Watts & Strogatz 1998)

The probability of a random connection was gradually increased from 0 (regular lattice) to 1 (random graph). Two characteristics of the resulting networks were then measured: path length, and clustering. These two measures are explained further in Box 4.4.

Box 4.4 Characteristic path length and clustering as two measures of complex networks (Watts & Strogatz 1998)

Characteristic path length L*:*

L is defined as the number of links in the shortest path between two nodes, averaged over all pairs of nodes.

Clustering coefficient C:

Suppose a node n has k_n neighbours. At most, $k_n(k_n\text{-}1)/2$ links can exist between them. This occurs when every neighbour of n is connected to every other neighbour of n. If C_n denotes the fraction of these allowable links that actually exist, then the clustering coefficient is the average of C_n over all n.

Watts and Strogatz found that path length and clustering reacted differently to increasing randomness. Path length dropped quickly whereas the amount of clustering dropped relatively slowly. Intermediate networks displayed high clustering but short path length. The term 'small-world' has come to describe these networks. A small-world network is depicted in Figure 4.5. Its most visible feature is its local clustering, the tendency of groups of nodes to be connected to each other. The short path length of small-world topology has been popularised as 'six degrees of separation' following experiments by the psychologist Stanley Milgram (1967). These showed that almost any two people in the USA could be linked by a series of no more than six acquaintances. The mean path length of this US acquaintance graph is probably underestimated, but it is clearly much less than would expected from, say, a regular lattice of 260 million nodes.

Figure 4.5 A small-world network (Jeong 2003)

4.5.3 Small world and scale-free

Many networks have been shown to display small-world properties. Some of these have also been shown to display a distribution of links that decays following a power law: for example the electric power grid for Southern California, the network of movie-actor collaborations, and the neuronal network of the nematode worm *Caenorhabditis elegans* (Barabási & Albert 1999), the world-wide web (Albert *et al*. 2000), and the network of citations of scientific papers (Seglen 1992; Redner 1998). Barabási and Albert dubbed these networks 'scale-free', by analogy with fractals where power laws arise and no single characteristic scale can be defined. Scale-free and a high degree of clustering, seemingly opposing tendencies, are reconciled in the concept of hierarchical modularity (Ravasz *et al*. 2002). In a hierarchical modular network there are many small, highly-connected modules that combine into larger units according to a power law. Small groups of nodes organize in a hierarchical manner into increasingly large groups, while maintaining a scale-free topology.

The power-law function of scale-free topology implies an infinite variance; in reality it means many nodes with few links and few nodes with many links (Strogatz 2001). Consider Figure 4.6. Figure 4.6a plots the frequency distribution of the number of links per

node (P_k) against the number of nodes (k) for a random graph of N=10,000 nodes. Such a plot is termed a 'degree distribution'. The degree distribution of random graphs follows a Poisson function, the exact form of which is dependent on the probability that any two nodes are connected (p). Figure 4.6b shows the degree distribution for the small-world network of Figure 4.5, plotted on logarithmic scales. The straight line that can be fitted to this plot follows a power-law function, $P_k \sim k^{-\gamma}$, with, in this case, $\gamma = 3$. A network with a degree distribution that follows a power-law decay, is termed scale-free.

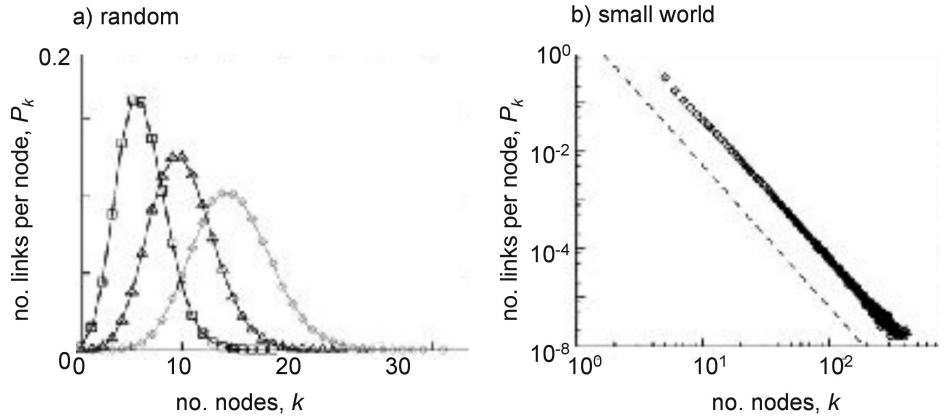


Figure 4.6 Degree distributions for a) random graphs of 10,000 nodes but different probabilities of connection (left , p = *0.005; middle,* p =*0.01; right,* p =*0.015); b) a small-world, scale-free network (Jeong 2003)*

Many real world networks display a scale-free degree distribution with power-law exponents that vary between ~1 and 2.5 (Albert & Barabási 2002); Tong *et al*. (2004) showed an exponent of 2.2 for metabolic networks. However real world networks can display other types of degree distributions, notably: 'broad scale' distributions, also termed 'truncated power-law', which show initially a power-law decay followed by a sharp cut-off in the tail, and 'single scale' distributions, such as exponential and Gaussian distributions, with fast-decaying tails (Amaral *et al*. 2000).

How do scale-free networks emerge? Barabási and Albert (1999) showed that power-law or similar degree distributions emerge automatically from a stochastic growth model in which new nodes are added continuously, attaching themselves preferentially to highly connected nodes or hubs. Preferential attachment is easily illustrated by considering the worldwide web. Any new site is more likely to establish links with existing, well-known, and already highly-connected sites, than with relatively obscure ones.

4.5.4 Scale-free and robust

Scale-free characteristics appear to be related to network robustness, and so indirectly to system stability. Robustness, together with its converse, fragility, is a measure of the ability of networks to resist fragmentation and secondary loss of its nodes. Fragmentation breaks down the web of interactions among nodes; it splits a network into sub-networks and, in the process, may trigger a cascade of node loss. It compromises the integrity of the original web of interactions and could represent a regime shift, with impli-

cations for future (co)evolution. As shown Figure 4.1, fragmentation can lead to remnant sub-networks, network breakdown, and system destruction.

Albert *et al*. (2000) observed that many complex networks display a surprising degree of tolerance against node loss. For example, the regular malfunction of key components of complex communication networks rarely lead to the loss of the global information-carrying ability of the network. Such error tolerance is often attributed to redundant wiring of the functional web defined by the systems' components. However Albert *et al*. demonstrated that error tolerance is not shared by all redundant systems. They found that scale-free networks displayed an unexpectedly high degree of robustness to random error, even in the face of excessively high node loss. The same networks also displayed extreme vulnerability to attacks on (i.e. removal of) the few hubs that play a vital role in maintaining the network's connectivity. This pattern of robustness and fragility differs from random graphs with Poisson degree distributions, which display similar responses to both random error and attack on the hubs (Strogatz 2001).

This basic pattern of robustness to random error and fragility to attack has now been demonstrated for a range of scale-free networks, including the Internet, metabolic and protein networks, and food webs (Albert *et al*. 2000; Jeong *et al*. 2000; Jeong *et al*. 2001; Solé & Montoya 2001). However the pattern may not be quite so straightforward. Maslov and Sneppen (2002) and Melián and Bascompte (2002) examined compartmentalisation within networks. The former showed that compartmentalisation within protein networks isolated the cascading effects of a deleterious mutation. Melián and Bascompte (2002) compared the same protein networks with three scale-free food webs that displayed less compartmentalisation. They argued that reduced compartmentalisation led to greater robustness with species or node loss, but at the same time greater susceptibility to the spread of a contaminant. Could it be that network topology reflects specific challenges that particular networks and systems have encountered?

Much work with network robustness focuses on node loss. Jain and Krishna (2002) examined the emergence of a new hub within a model system in which populations of molecular species coevolve with their network of chemical interactions. Successful new species that eventually became hubs also caused secondary extinctions and partial fragmentation. The analogy they draw for this process is the appearance of the automobile, which created new industries and promoted the growth of some existing ones, but made the horse-drawn carriage and its ancillary industries obsolete.

4.6 Food webs as complex networks

4.6.1 Small world and scale-free?

A community is simply defined in ecology as an assemblage of populations occurring together in space and time. However ecologists have long recognised that the emergent features of a community do not derive from co-occurrence, but from interaction. Feeding interactions have received the bulk of attention; d food webs map these interactions. Food webs are interconnected chains where consumers have a negative effect on the consumed (i.e. decrease their growth rates) and the consumed have a positive effect on their consumers (i.e. increase their growth rates). Food webs are hierarchical, and usually

depicted so that positive effects are bottom-up and negative effects are top-down. While there are potentially many levels within the hierarchy, the majority, approximately 80% in the food webs studied by Williams *et al*. (2002), of species within a community fall into one of three trophic levels: a basal level comprising carbon-fixing producers and carbon available for recycling in detritus; an intermediate level feeding primarily on the basal level (termed primary consumers or herbivores); and, a top level feeding primarily on the intermediate level (termed secondary consumers or carnivores).

Despite early suggestions that food webs were both the small-world and scale-free (e.g. Solé & Montoya 2001), recent investigations suggest otherwise. Williams *et al*. (2002) confirmed small path lengths after assessing seven of the largest, most comprehensive, and highest quality empirical food webs in the primary literature. Species within these large communities from a variety of aquatic and terrestrial ecosystems were on average two links apart, with >95% of species typically within three links of each other. These results contrast with earlier research using poorly resolved and highly aggregated food-web data that led Schoener (1989) to speculate that path lengths would increase with greater species richness. The results of Williams *et al*. suggest that this is not so, and that species within ecosystems may be more highly interconnected than previously thought.

Camacho *et al*. (2002) and Dunne *et al*. (2002a) report low, not high, clustering. Dunne *et al*. compared clustering coefficients (see Box 4.4) for 16 food webs and compared them with counterpart random webs. Only four food webs displayed clustering that was more than twice that of random webs; six food webs displayed clustering less than that of random webs (see Appendix I at the end of this chapter). They suggested that food webs might generally be too small to display clustering. The ratio of actual to random clustering coefficients increased linearly with network size; a 1:1 ratio occurred in networks of about 40 nodes.

Initial investigations into food webs, notably the three well-documented food webs of Ythan estuary, Silwood Park, and Little Rock Lake, confirmed scale-free characteristics (Solé & Montoya 2001). Further investigations seem to have reversed this conclusion. Camacho *et al*. (2002) studied seven webs and found only single scale distributions. Dunne *et al*. (2002a) investigated 16 food webs, including those of Solé and Montoya and Camacho *et al*, to find: that degree distributions were scale-free in only one case; a second web displayed a truncated power-law distribution (broad scale): and the remaining webs displayed exponential or uniform distributions (single scale). Their results are reproduced in Figure 4.7.

Few other interaction networks among the species comprising ecological communities have been examined. An exception is the non-symbiotic, plant-animal mutualistic networks investigated by Jordano *et al*. (2003). Such networks, unlike food webs, do not necessarily track energy flows. Two such networks investigated by Jordano *et al*. include plants and their pollinators, and plants and seed dispersers. The results contrast with those of Dunne *et al*. and Camacho *et al*. in that Jordan *et al*. found more evidence for scale-free, or at least broad scale, degree distributions.

The conclusion to date is that, while food webs display short path lengths, their generally low level of clustering and predominance of single scale degree distributions suggest that they are neither small-world nor scale-free.

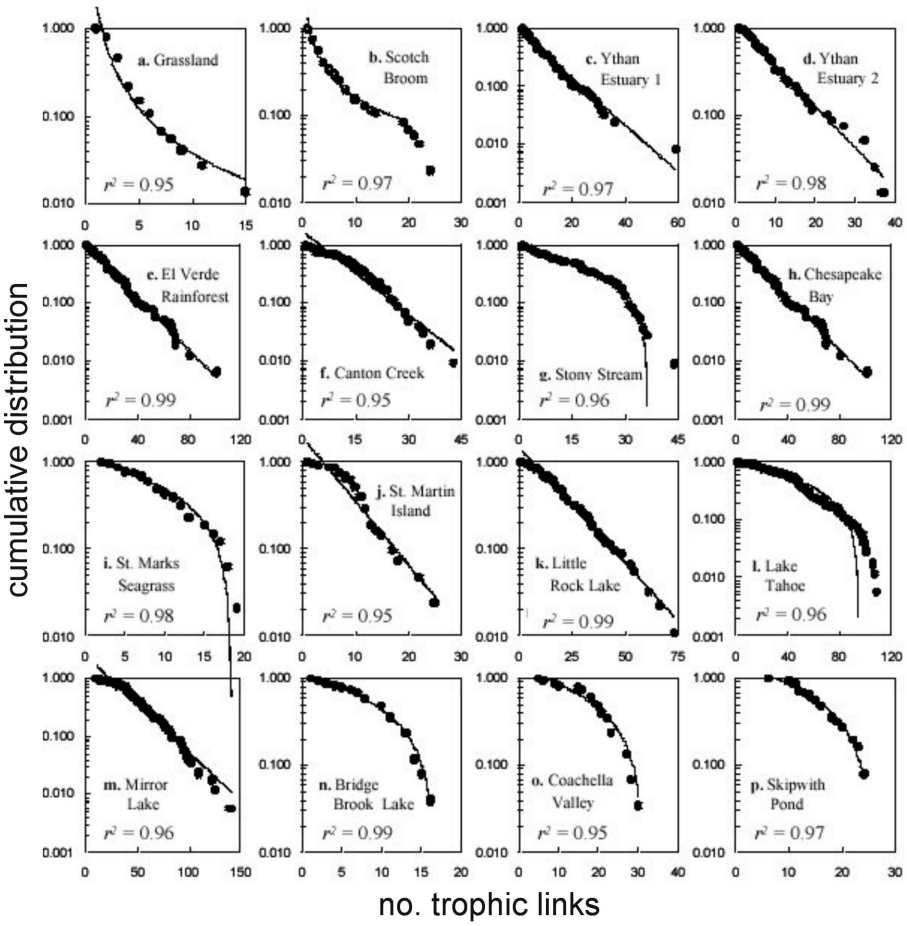


Figure 4.7 Linear-log plots of the cumulative distributions of links per species in 16 food webs. Lines and r^2 *values show the best fit to one of three simple models: power-law (upward curved line,) exponential decay (straight line), or uniform (downward curved line) (Dunne* et al. *2002a)*

4.6.2 How do food webs grow?

Barabási and Albert (1999) proposed two generic mechanisms for the creation of scale-free networks: stochastic growth with addition of nodes and links, and preferential attachment of new nodes to existing hubs. Early investigations into food webs showed that they were scale-free, and so led to questions as to whether these two mechanisms apply to food webs. Dunne *et al*. (2002a) argued that the simple growth mechanism is clearly violated in food webs since there are both additions and losses of nodes at ecological and evolutionary time scales via immigration, emigration, speciation and extinction. The net effect of such changes can be expansion, contraction or no change in either number of nodes or number of links. The first mechanism is absent.

Do species attach preferentially to hubs? A species may have many consumers because it is relatively abundant, and its abundance may make it more likely to serve as prey for a new species. This 'abundant-get-eaten' mechanism supports the notion of preferential attachment. Jordano *et al*. (2003) found a significant correlation between abundance and the number of links in plant-seed dispersal networks. Despite this, they found a predominance of broad scale rather than scale free degree distributions.

Other authors query preferential attachment. Investigations by Camacho *et al*. (2002) led these authors to suggest that specialisation limits species' choice of prey. Jordán and Scheuring (2002) questioned preferential attachment, arguing that ecological reality would suggest the contrary if food were the main limiting factor to the incoming species. Dunne *et al*. (2002a) argue that there is little data to suggest that invasive consumers tend to prey on species that already have a large number of consumers. Theoretically, competitive exclusion would cause overlapping niches to repulse each other, reducing the average number of consumers preying upon resource species.

Support for preferential attachment can be gleaned from a wide range of studies suggesting that generalist consumers are more likely to prey on invasive species than specialist consumers (various references in Dunne *et al*. 2002a). However, an invasive species might be more likely to establish successfully if it has few consumers. In support of this hypothesis, Dunne *et al*. offer initial data from Hawaii that suggest that there are more successfully-established alien parasitoids than alien herbivores or plants. Parasitoids would be expected to have fewer consumers.

There is general agreement that there are constraints to the establishment of new nodes in food webs, that this may compromise both mechanisms proposed by Barabási and Albert (1999), and perhaps that this might explain the predominance of broad and single scale degree distributions. A number of such constraints have been offered. Amaral *et al*. (2000) showed how the inclusion of 'aging', where some nodes cannot accept new links, and 'cost', where there is a maximum number of possible links per node, could eliminate scale-free topology. Jordano *et al*. (2003) adds a third constraint – 'forbidden links'. They argue that the biological attributes of species can provide barriers to interaction. To illustrate, the seeds of a winter-ripening plant cannot be dispersed by a frugivore that is a summer stopover migrant; polar bears do not eat penguins; tigers do not eat trees.

The tentative conclusion would be that mechanisms for generating scale-free networks are absent or, at best, only weakly evident in food webs. This may explain why few food webs appear to display scale-free characteristics. However, the point about being scale-free relates to patterns of robustness and fragility.

4.6.3 Why are food webs fragile to hub loss?

Scale-free networks with highly skewed power-law degree distributions are fragile to attack on the hubs while being relatively robust to random error. Solé and Montoya (2001) confirmed this pattern for three, scale free food webs. Fragmentation occurred only with an very large number of random removals. Secondary extinctions, whereby the random removal of a species led to a subsequent or cascading loss of other species, were rare. However, the three webs were extremely vulnerable to the removal of highly-connected species or hubs. The food webs fragmented and suffered secondary extinctions.

Dunne *et al*. (2002a and b) extended this analysis. The latter publication showed that, even though most of their food webs did not display power-law degree distributions, they still displayed fragility to attack and robustness to random species loss. The response to node removal is obviously not unique to scale-free networks. Dunne *et al*.'s analysis provided greater insight into food web fragility. They argued that fragility to hub removal makes both topological and ecological sense. The greater the number of

links of a species relative to other species in the web, the more likely that its loss will have a significant impact on ecosystem structure and function. The short path length of food webs means that the loss of a highly connected species will have direct and indirect effects that could easily encompass the vast majority if not all of the species in the web.

Yet, fragility varied across the 16 food webs analysed. Dunne *et al*. (200b) quantified robustness as the fraction of primary species removals resulting in the loss of more than 50% of species (both primary removals and secondary extinctions). They correlated robustness following hub removals with three measures: species richness, connectance and omnivory. Species richness is simply the total number of species. Connectance is the fraction of all possible links among components of a network that are realised. Omnivory was measured as the fraction of species that feed at multiple trophic levels. Box 4.5 outlines the general pattern of robustness and connectance.

Box 4.5 Connectance and robustness for food webs investigated by (Dunne et al*. 2002b)*

1. Low connectance ($C < 0.06$*)*

Silwood Park is a 'source' web based on a single basal species, the Scotch broom (*Cytisus scoparius*). This species is inevitably a hub, and its removal had a predictable and severely disruptive effect on the food web. The Ythan estuary food webs, while not source webs *per se*, still have very few basal species. Their removal also led to severe disruption of the web. If hub removal sequences excluded basal species, the response of these three webs was similar to that of the grassland, shown by Dunne *et al*. (2002a) to be scale-free. Fragility to hub removal was very clear for these four webs where removals of about 20% of highly-connected species led to about 60-100% of species going extinction.

2. Medium connectance ($0.10 \leq C \leq 0.15$*)*

The response of webs with a medium connectance to sequences of random and highly-connected removals hardly differed until about 20% of all species had been removed. Secondary extinctions then increased rapidly with the removal of highly connected species, while random removals triggered only a gradual increase in secondary extinctions.

3. High connectance ($C \geq 0.15$*)*

The four webs with highest connectance displayed low levels of secondary extinctions to sequences removing both highly-connected and random species until about 40% of primary removals, at which point secondary extinctions increase faster for hub removals.

Greater robustness to hub removals correlated with food web connectance – the higher the connectance, the greater the proportion of hubs that must be removed to trigger secondary extinctions. Robustness and connectance were correlated logarithmically, following curves that saturate at about 0.3 connectance. This is the upper bound for empirically observed food web connectance values. The robustness curves for the removal sequences of the most connected species with and without basal species removals have a similar slope. However, not removing basal species led to additional robustness at any particular connectance level, with about 10% additional primary species removals required to achieve the same level of total species loss.

4.7 Conclusions

This chapter has drawn on a range of disciplines and research themes to take coevolution a step further, from between species to within and between systems. It reemphasises that interactions are central to coevolution. It highlights the complex pattern of interactions

among components of systems and goes further than Chapter 3, which examined only one interaction between pairs of species or species groups.

Research into complex systems is relatively recent. The notion that complex systems evolve and coevolve has captured the imagination of many scientists from many disciplines. My focus on interactions between and within systems lead me to highlight the even more recent research into complex networks. Complex networks map the interactions among components of complex systems. Given the key role of interaction in coevolution, complex networks might offer a means of examining how changes to the pattern of interactions might influence the possible future states of a system.

Research into complex networks has yielded a number of characteristics that are common to many networks. Experiments have shown that the removal of nodes has varying effects on a network's robustness and that the effect is determined by network topology. Food webs provide an example of a complex network. Initial research suggests that food webs display different characteristics, yet exhibit follow the general pattern of many poorly-connected and a few highly-connected nodes, and robustness to random loss with fragility to targeted attack on hubs. The work of Dunne *et al*. (2002b) is crucial here as some food webs display robustness in the face of attack on hubs. Robustness correlated with connectance, a measure of topology.

The hallmark of social impact is the loss of species, as was discussed in Chapter 2. I pose a number of questions.

- Is social impact targeting poorly- or highly-connected species?
- How are we affecting the robustness of ecological systems?
- How are ecological systems affecting the robustness of social systems?
- How is human intervention into ecosystems affecting the network of interactions among the actors of social systems and the species of ecological systems?

The remainder of this dissertation addresses these questions. Dunne *et al*. (200b) used connectance to compare food web response to node loss. Chapter 5 examines what happens to the connectance of a food web as nodes are lost. It addresses the question of whether changes to connectance indicate changes to network robustness and the likelihood of fragmentation and secondary loss of species.

The node removal protocols used by Dunne *et al*. (200b) bear little or no relationship with real-world loss of species. There is no *a priori* reason why species loss should be random, should be targeted on hubs, or should exclude basal species. Chapter 6 begins by examining each of the sources of social impact from Chapter 2 from a network perspective. It attempts to specify which species are under threat from social impact, what their role (position and connectedness) in food webs might be, and what effect their loss might have on food web robustness.

Chapter 6 not only introduces social systems by considering social impact on food webs, but it also addresses specification of the reciprocal effects of species loss. The notion of a socio-natural network is introduced. Such a network incorporates interactions within and between an ecological system and the human activities that transact its products. Construction of a socio-natural network is the first step in my application of topological analysis to environmental management, illustrated by the case study in Chapter 7.

Appendix I. Topological properties of food webs, listed in order of increasing connectance (Dunne et al. 2002a and b)

Food web[1]	Taxa[2]	Resolution[3]	Species richness (S)	Characteristic path length (D)	Clustering coefficient relative to random graph (C/C_{ran})	Degree distribution	Connectance (L/S^2)	Average node degree ($k = 2L/S$)	Omnivory (O)
Grassland	75	100	61	3.74	--	Power law	0.026	3.18	0.21
Scotch broom	154	99	85	3.11	3.0	Power law	0.031	5.24	0.28
Ythan Estuary 1	134	86	124	2.34	3.8	Exponential	0.038	9.34	0.62
Ythan Estuary 2	92	86	83	2.20	2.7	Exponential	0.057	9.52	0.53
El Verde Rainforest	156	49	155	2.20	1.4	Exponential	0.063	19.48	0.56
Canton Creek	108	94	102	2.27	0.3	Exponential	0.067	13.66	0.08
Stony Stream	112	89	109	2.31	0.4	Uniform	0.070	15.22	0.11
Chesapeake Bay	33	55	31	2.65	1.0	Exponential	0.071	4.38	0.52
St. Marks seagrass	48	71	48	2.04	1.3	Uniform	0.096	9.20	0.71
St. Martin Island	44	34	42	1.88	1.1	Exponential	0.116	9.78	0.60
Little Rock Lake	182	93	92	1.89	2.1	Exponential	0.118	21.68	0.38
Lake Tahoe	800	99	172	1.81	1.1	Uniform	0.131	45.18	0.58
Mirror Lake	586	96	172	1.76	0.9	Exponential	0.146	50.26	0.59
Bridge Brook Lake	75	95	25	1.85	0.8	Uniform	0.171	8.56	0.40
Coachella Valley	30	3	29	1.42	1.3	Uniform	0.312	19.06	0.76
Skipworth Pond	35	91	25	1.33	1.0	Uniform	0.315	15.76	0.60

1 See Dunne *et al*. (2002a) for sources of information on the respective food webs.

2 Number of compartments in the original food web, ranging from ontogenetic stages (e.g. juveniles versus adults), to non-phylogenetic categories (e.g. detritus, seeds) to highly aggregated taxa (e.g. microbes).

3 Refers to the percentage of taxa identified to the genus or species level.

5. The Robustness of Ecological Networks

"And in that moment he knew that, despite the apparent beetle fixation, here *was where he'd always wanted to be, at the cutting edge of the envelope in the fast lane of the state of the art.*

"The Last Continent", Pratchett 1998, p228

5.1 Introduction

State-of-the-art knowledge among ecologists and those investigating complex systems suggests a direct relationship between the pattern of interactions among system components and the stability of complex adaptive systems (see Chapters 2 and 4). The study of the network topology has led to a number of measures of their pattern. Certain topological features are common to some, maybe many, complex networks (see Chapter 4). The particular stability concept addressed when examining network topology is robustness.

Robustness is defined in terms of a network's ability to resist fragmentation and/or secondary loss of nodes. Its converse is fragility. Robustness is similar to Pimm's definition of resistance (see Table 2.2), in that a robust network resists fragmentation. Fragmentation is a breakdown of a network into sub-networks. Connectedness is disrupted, although this can occur to varying degrees. Consequently robustness is also similar to Holling's definition of resilience (see Table 2.2 and Chapter 4). A robust network maintains is structure and resists change, and so is arguably both stable and resilient.

Complex networks with small-world and scale-free properties have shown a consistent pattern of being robust to random error but fragile to attack on highly-connected nodes, or hubs. Dunne *et al*. (2002a & b) examined 16 food webs in an attempt to apply this relatively recent analysis of network topology to food webs (see Chapter 4). The first of these papers showed that the food webs displayed less clustering than would be expected of small-world networks, and that they were generally not scale-free. The second paper showed that food webs still displayed robustness against random error and fragility to attack. The main contribution to our understanding of network topology and robustness

from this study was that robustness varied, and correlated, with network connectance. Food webs with a higher connectance were more robust to targeted attack.

Connectance is one way of measuring connectedness (see Section 5.2 and Figure 5.2). Holling uses connectedness on the *x*-axis of his adaptive cycle (see Chapter 4). As systems move through the growth and conservation phases of this cycle, their connectedness and stability increase. At the same time, dependence on the structure of interactions increases so that resilience decreases (Peterson 2003). It is hard to place robust food webs, displaying stability and resilience and with a high connectance, within this framework. Admittedly connectedness is more than connectance. Connectance records the number of realised interactions, not their structure, nor a system's dependence on structure. Structure would seem to equate to pattern, or to network topology. Dependence may relate to the distribution of strong and weak links (see Chapter 2).

Connectance has a long history in ecology. Its main use has been in food web research, the goal of which is to find universal quantitative patterns in food webs and so to discover general principles of ecology (May 1983 & 1988; Cohen 1989 in Martinez 1992). Consequently it is used to compare different ecological communities. Ecological food web research also deals with the issue of stability. It has studied the effects of perturbation and examined the properties of food webs that confer stability.

If connectedness lies behind stability, and if it is the product of past coevolution as would be argued by those studying complex systems, then changes in the pattern of interactions would seem to have implications for both stability of the system and possible directions for its future coevolution. Measures of connectedness, such as connectance, may provide clues as to the future direction of coevolution subject to stress or perturbation. Is a network at greater risk of fragmentation and secondary extinction as a result of social impact or human (mis)management? Is future coevolution likely to be characterised by abrupt shifts in system state? Can anticipated future states of the same network be compared with regards to this risk? These questions are central to the analytical framework I am developing in this dissertation.

Figure 5.1 depicts the goal of this chapter, which is to assess whether changes in network topology could indicate changes in the robustness of an ecological network. The figure shows an ecosystem as a complex adaptive system where feeding interactions among components are represented as a network. The system also interacts with its environment and components of other systems. The loss of species from, and/or the addition of species to, the network changes its connectedness, indicated in this figure as ΔC. Characteristics of the original network and the magnitude of change to connectedness may indicate reduced network robustness, and in turn a greater propensity to lose nodes secondarily and/or to fragment. Secondary losses and fragmentation, in turn, indicate that a new trajectory of growth, development and coevolution may emerge.

Specific objectives of this chapter are:

- to elaborate on connectance and its behaviour as a measure of the interconnectedness of a system's components;
- to generalise the relationship between connectance and a change in the number of species in a food web; and,
- to relate robustness and network topology with species removal from a food web.

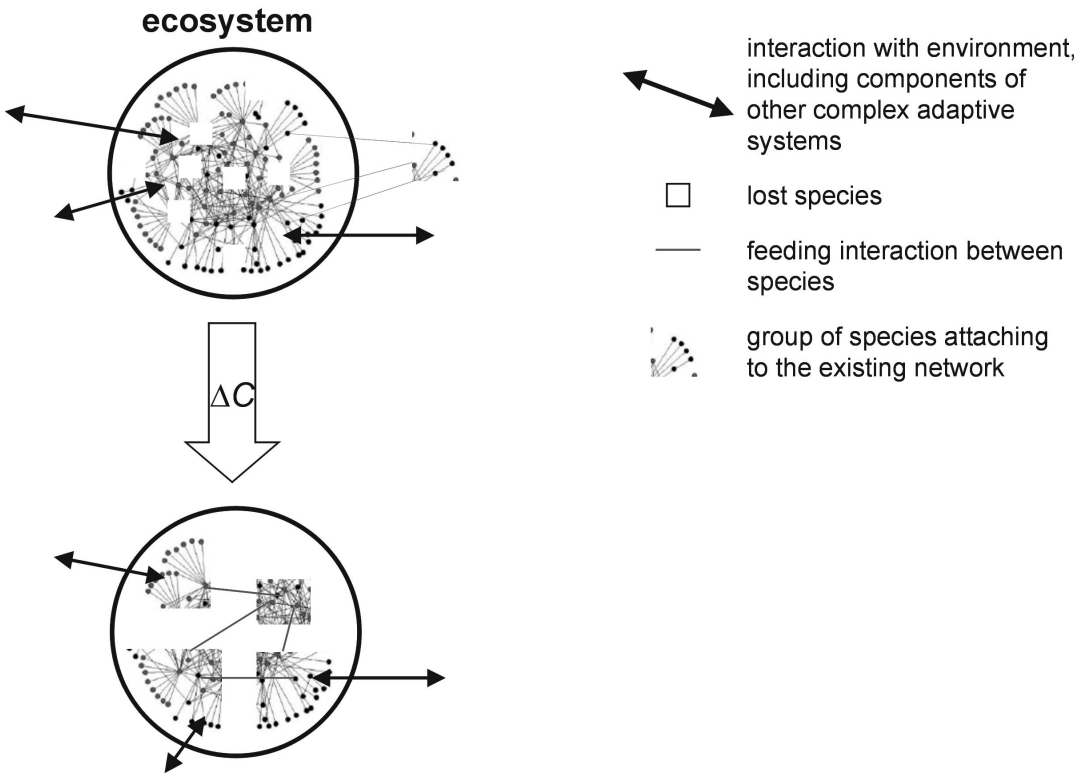


Figure 5.1 Measures of network topology, such as change in connectance (ΔC), could indicate the response of a food web to species loss and addition

These objectives are addressed in Sections 5.2-5, with conclusions drawn in Section 5.6. I focus on food webs and species loss, extending the work of Dunne *et al*. (2000a and b). My particular perspective is the loss of biodiversity as a general consequence of social impact on natural ecosystems. An aspect of the sustainable development debate is concern that ecosystem stability is being compromised, and that possible shifts in system structure and function would have consequences for the future supply of environmental goods and service, and affect the coevolution of natural and social systems.

5.2 The meaning of connectance

5.2.1 Connectance as a measure of network topology

Connectedness is a general term describing the degree to which components of a system are affected by each other (Allen & Starr 1982 in Martinez 1991). Holling uses it as the *x*-axis of the adaptive cycle (see Figure 4.3). Its application in ecology focuses almost exclusively on feeding interactions. Different perspectives of connectedness are summarised in Figure 5.2 and elaborated below.

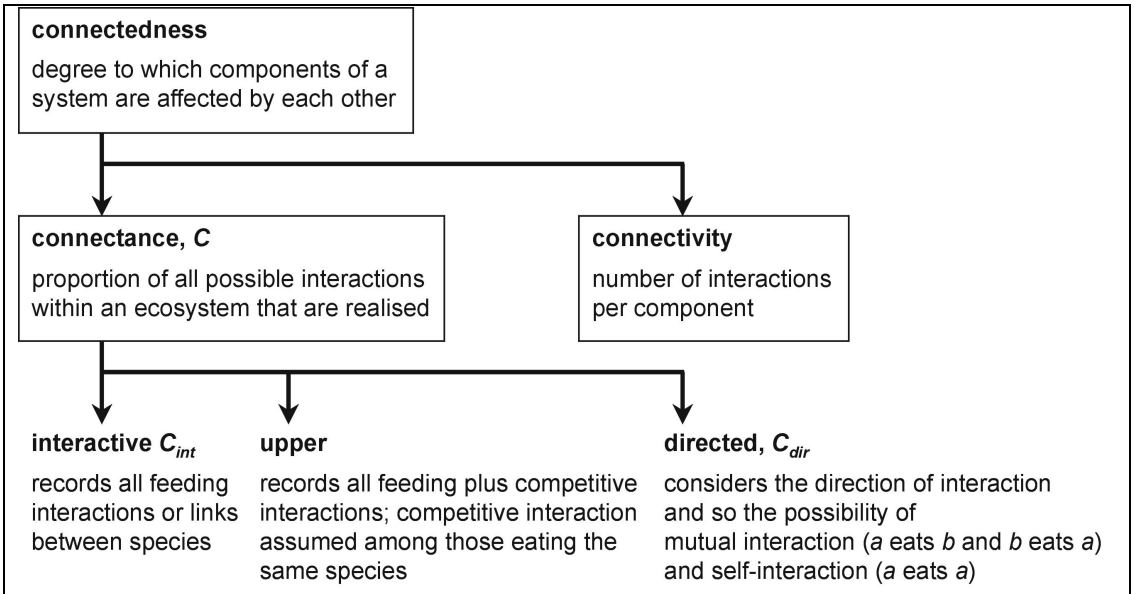


Figure 5.2 Perspectives on connectedness and their definitions

Martinez (1991) delineates two aspects of connectedness that have been described in the ecological literature (various references). Connectivity refers to the number of interactions per component, while connectance refers to the proportion of all possible interactions, or links, that are realised (Gardner & Ashby 1970). Martinez (1991) showed that connectance, and particularly directed connectance, was the most robust[1] measure of connectedness when confronted with different levels of resolution of food web data. Resolution relates to the degree to which different components are distinguished from each other.

As shown in Figure 5.2, there are three different versions of connectance within ecology: interactive, upper and directed connectance. Interactive and directed connectance are elaborated below. Upper connectance is based on interactive connectance but includes competitive as well as feeding interactions. It assumes that those eating the same species are in competition. Upper connectance has been excluded from further consideration because this assumption is questionable, because competition between species stems from more than just feeding interactions, and because it adds only one of possibly many types of interaction between organisms. The focus here is on feeding interactions.

Interactive connectance records the presence of interaction between two components of a food web. Directed connectance considers the direction of interaction, and so includes the possibility of mutual interaction (*a* eats *b* while *b* eats *a*) and self-interaction or cannibalism (*a* eats *a*). This leads to differences in how the maximum number of possible interactions is calculated, as illustrated in Figure 5.3.

[1] Use of 'robust' here is in the sense of being strong enough to withstand intellectual challenge.

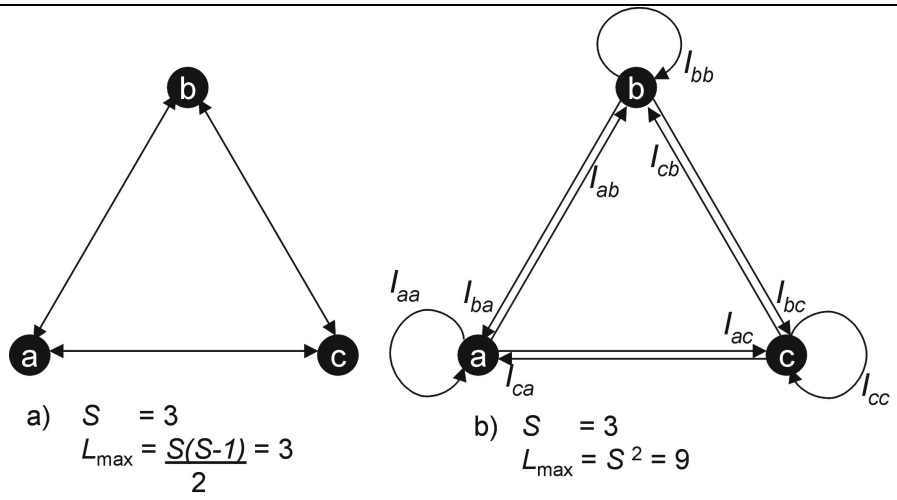


Figure 5.3 Interactive (a) and directed (b) connectance illustrated for a 3-node network

The formulae for interactive and directed connectance are, respectively:

$$C_{int} = \frac{2L}{S(S-1)} \qquad \text{Eq. 5.1, and}$$

$$C_{dir} = \frac{L}{S^2} \qquad \text{Eq. 5.2}$$

where

C_{int} and C_{dir} = interactive and directed connectance respectively;
L = number of feeding interactions or links between pairs of species; and,
S = number of species (or nodes) in the network.

The same equations may be found in network literature in general. Martinez (1991) argued that the better performance of directed connectance relative to interactive connectance was due to its better representation of ecological reality. Cannibalism in particular is common in some ecosystems and it may be underestimated in many food webs (Polis, 1991; Dunne *et al*. 2004, 2005). Such detail in the direction of interaction may not be necessary in other complex networks. For example mutual interaction is not relevant for social networks since if *a* knows *b*, it may be generally assumed that *b* knows *a*; self-interaction would seem to be irrelevant for telephone networks. The choice of formula for connectance will depend on the nature of the interaction captured in a network.

5.2.2 The behaviour of connectance

Both formulae for connectance suggest that connectance is continuous, varying smoothly between 0 and 1. This is not so because L and S are integers and cannot vary independently from each other. Only for large S can connectance be viewed as varying smoothly, as is shown below.

The minimum value of connectance is never zero. Zero connectance means zero links, and zero links means that there is no network, just an assemblage of non-interacting nodes or species. The minimum value of connectance for a network derives from the minimum number of links required for *S* nodes to form a network. This minimum number generalises to *S*-1, as illustrated in Figure 5.4.

Figure 5.4 shows different combinations of interactions among six nodes or species. In Figure 5.4a there is no network of six species. There are two networks, one of four and one of six species. No meaningful connectance can be calculated for a network of these six nodes. Figures 5.4b and c show the base configurations for minimum connectance, viz.: a chain with sequential links, and a species that interacts with all other species. Each is a network of six nodes with five (*S*-1) links. Other variations based on five links and six nodes are possible, such as that shown in Figure 5.4d. Self-interaction (e.g. cannibalism), cross-links between chains, and the closed loops (Figures 5.4e, f and g) increase the number of links above the minimum.

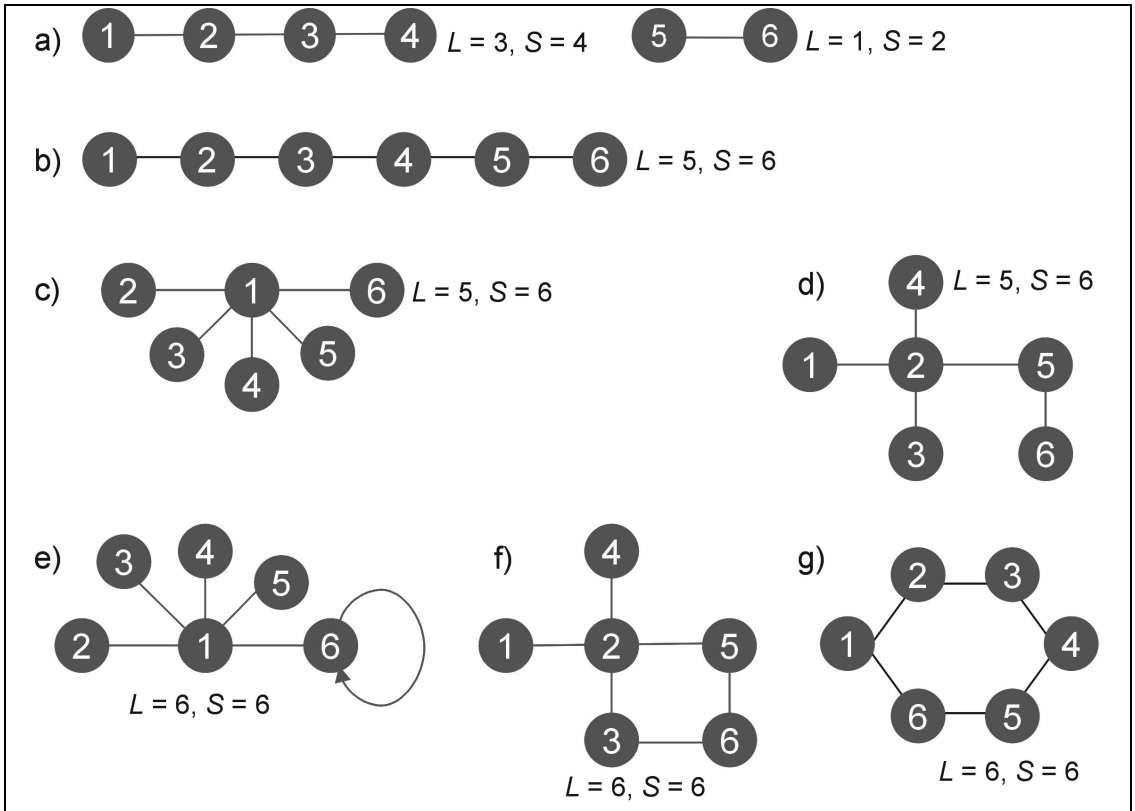


*Figure 5.4 Various configurations of networks comprising six nodes: a) insufficient links for a 6-node network; b), c) and d) three configurations for minimum connectance (*L = N-*1); e) self-interaction (e.g. cannibalism); f) cross-linked chains; and g) a loop*

Very different networks may have the same *L* and *S*. The number of realised interactions captures only a part of the pattern of interactions in a network.

Meaningful values of connectance vary between a minimum value dependent on network size, *S*, and 1 where the maximum number of links is realised. The minimum value approaches zero as *S* approaches infinity. The maximum value is always 1, where all possible links are realised. Maximum and minimum values of connectance for networks of up to 200 species are shown in Figure 5.5. Connectance has no meaning when its value falls under the line denoting the minimum *C*. The number of links is too small for the species to form a network.

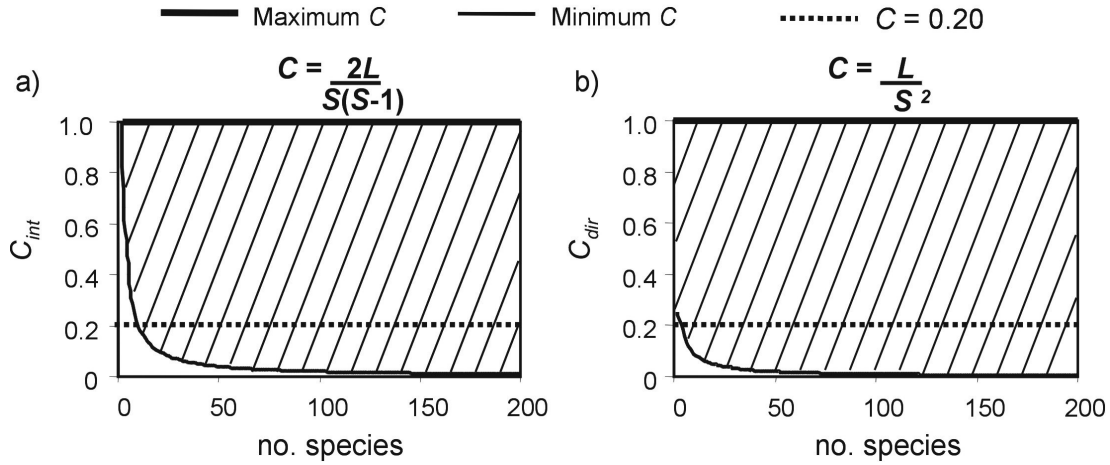


Figure 5.5 Realistic values of connectance (shaded) vary between a maximum and a minimum for any S*: a) interactive connectance and b) directed connectance*

A line has been drawn on each graph in Figure 5.5 at $C = 0.2$. The same value of connectance may not mean the same to networks of different sizes. Consider the left hand graph. A connectance of 0.2 has no meaning for a network of, say, 5 species. At S=10 it equates with the minimum possible value of connectance. As S increases, this value of connectance become more intermediate between the minimum and maximum values. At high S the position of a connectance of 0.2 between the maximum and minimum hardly differs for different S. This means that it is valid to compare only networks of a similar size, or of a large size, with regards to their connectance.

While Martinez (1991) discusses the minimum value of connectance, he does not draw my conclusion, which is that values of connectance should be standardised to lie between 0 and 1. Only with standardisation does the same value mean the same for networks of different sizes. Standardisation is performed using the following equation:

$$C_{\text{stand}}(s) = \frac{C(s) - C_{\min}(s)}{1 - C_{\min}(s)} \qquad \text{Eq. 5.3}$$

where *(s)* denotes that connectance relates to networks with the same number of species.

Standardisation should precede comparison of different networks, particularly if the networks have low *S* and/or are of very different sizes. The transition between low and high *S* is somewhat arbitrary, but Figure 5.5 suggests around 100 species for interactive connectance, and around 50 species for directed connectance.

Connectance is not continuous for another reason – because *L* and *S* are integers and do not vary independently from each other. There are discrete values of connectance for networks of a given size. The effect of this is severest for small *S* as shown in Figure 5.6 where connectance can only take on the values indicated. Standardisation spreads these points between 0 and 1, but discrete values for connectance remain.

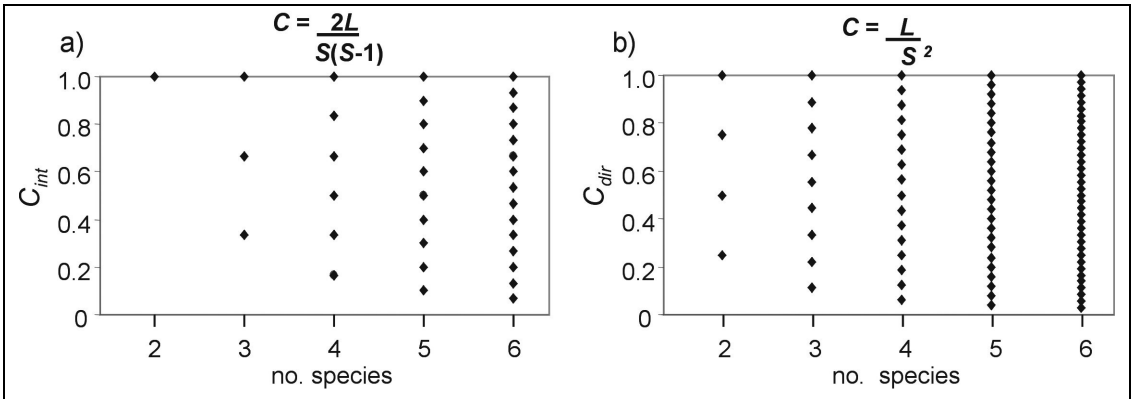


Figure 5.6 Discrete values that connectance may assume at low S*: a) interactive connectance and b) directed connectance*

Values of connectance at very low *S*, i.e. less than about 10 species for interactive and less than about 5 species for directed connectance, should be treated with extreme care. Ecologists are generally aware of the difficulties of working with food webs with less than about 20 taxa because there are many methodological problems with low-diversity representations of ecosystems. Below about 10 species, food webs are poor representations of the system under study, although difficulties are attributed more to high aggregation and low resolution (Martinez 1991). The inconsistent behaviour of connectance at low species richness only compounds these problems.

Of the two formulae for connectance, directed connectance is less sensitive to species number and to discrete values for *L*. My analysis supports Martinez in his preference for directed connectance. However, I also argue for standardisation, especially if the connectance of different networks are to be compared. The connectance of very small networks should be disregarded, or at least treated with extreme care. Only standardised, directed connectance is considered further.

5.2.3 Implications of standardisation

Dunne *et al*. (2002b) showed that robustness correlated with connectance. The correlation compared the proportion of primary species removals required to induce a total loss (primary removals plus secondary extinctions) of 50% or more of the species in each of 16 food webs as a function of the connectance of each web. Dunne *et al*.'s discussion of results focused on food webs' responses to the loss of highly connected species. Food webs were contrasted with scale-free networks. More connected food webs were not only less likely to be scale-free (Dunne *et al*. 2002a), but also less fragile to hub loss.

Figure 5.7 reproduces the Figure 1 from Dunne *et al*. (2002b). The horizontal axis shows primary removals as proportions of the total number of species, and the vertical cumulative secondary losses as proportions of the total number of species. Food webs are ranked according to their connectance, from lowest (Grassland, a) to highest (Skipwith Pond, p). The trend towards fewer secondary extinctions and so greater robustness with increasing connectance can be seen in that the plots become flatter moving from (a) to (p). While this trend becomes somewhat erratic in the food webs with highest connectance, the main inconsistency lies with the Chesapeake Bay food web (Figure 5.7h). This

food web has a connectance similar to Canton Creek and Stony Stream (Figure 5.7f and g), yet its secondary losses are greater for all removal sequences.

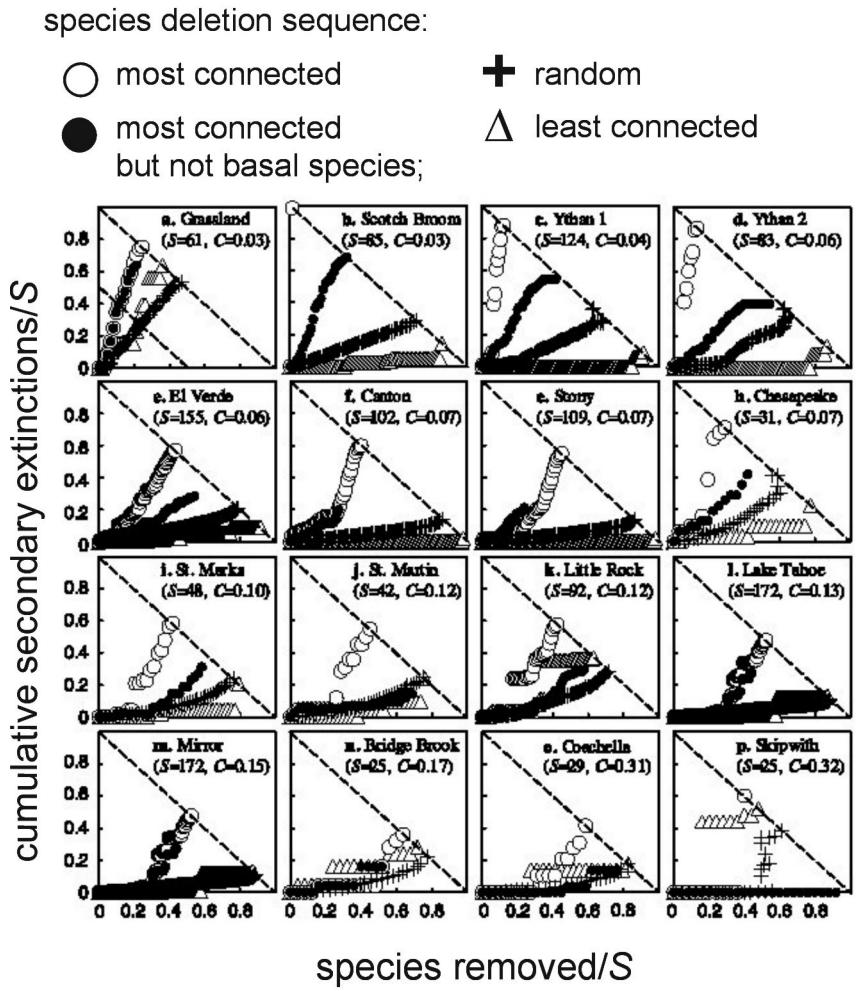


Figure 5.7 Response of 16 food webs to four species removal protocols (Figure 1, Dunne et al. *2002b)*

Table 5.1 shows the 16 food webs, in the same order as Figure 5.7, together with their species number, directed connectance, standardised directed connectance, and a new ranking based on standardised connectance. Food webs that would be ranked differently using standardised connectance are highlighted. Chesapeake Bay has few species relative to Canton Creek and Stony Stream. Standardisation changes its rank considerably and places it between the two Ythan Estuary webs. Its behaviour with regards secondary losses is visually more similar to these two webs – higher secondary losses with both random hub removals – than to either Canton Creek or Stony Stream. This suggests that standardisation of connectance would improve the correlation between robustness and connectance.

Table 5.1 Effect of standardisation on the ranking of 16 food webs; food webs with altered rank are highlighted

Old rank	Food web	Species richness (S)	Connectance (C)	Standardised Connectance (C_{stand})	New Rank
1	Grassland	61	0.026	0.010	1
2	Scotch broom	85	0.031	0.020	2
3	Ythan Estuary 1	124	0.038	0.030	3
4	Ythan Estuary 2	83	0.057	0.046	5
5	El Verde Rainforest	155	0.063	0.057	6
6	Canton Creek	102	0.067	0.058	7
7	Stony Stream	109	0.070	0.062	8
8	**Chesapeake Bay**	**31**	**0.071**	**0.041**	**4**
9	St. Marks seagrass	48	0.096	0.077	9
10	St. Martin Island	42	0.116	0.095	10
11	Little Rock Lake	92	0.118	0.108	11
12	Lake Tahoe	172	0.131	0.126	12
13	**Mirror Lake**	**172**	**0.146**	**0.141**	**14**
14	Bridge Brook Lake	25	0.171	0.138	13
15	Coachella Valley	29	0.312	0.288	16
16	**Skipwith Pond**	**25**	**0.315**	**0.288**	**15**

Standardisation also changes the ranking of the four webs with highest connectance. Unlike Chesapeake Bay, it is difficult to argue that standardisation has led to greater conformity with the trend linking robustness and connectance. The main feature of the plots for these four webs in Figure 5.9 is that the webs appear to resist secondary losses up to an apparent presence of threshold. Skipwith Pond (Figure 5.9p) displays an abrupt 'flip' from no to quite substantial secondary losses. However these thresholds lie outside the range of data used by Dunne *et al*. (2000b) to correlate robustness with connectance.

This section has not only argued that standardisation of connectance is required, particularly in food web research characterised by relatively small networks (nearly half of the food webs above comprise less than 50 species, and 50 nodes was identified above as the approximate transition between reliable and unreliable behaviour of connectance), but also that it may change, even improved, our insights into the relationship between stability and connectedness.

5.3 Change in connectance with changes in species number

5.3.1 Introduction

In contrast to the work done by Dunne *et al*. (2002a and b), my focus lies with changes in connectance within a network, rather than a means to compare networks. This section examines theoretical changes to connectance with the loss and gain of species. Such changes for two food webs are analysed further in Section 5.4. The section ends with a brief discussion on the growth of networks.

5.3.2 Loss of species

The loss of species from a food web reduces both the number of species and the number of links, and so can effect a change in connectance. The magnitude of change caused by the loss of one species from a food web is explored in Figure 5.8. The food web initially comprises 156 species and 1518 links and has a standardised, directed connectance of 0.056. The number of links lost when one species is lost depends on how connected it is. The figure examines the change in connectance for a loss of 1 to 80 links.

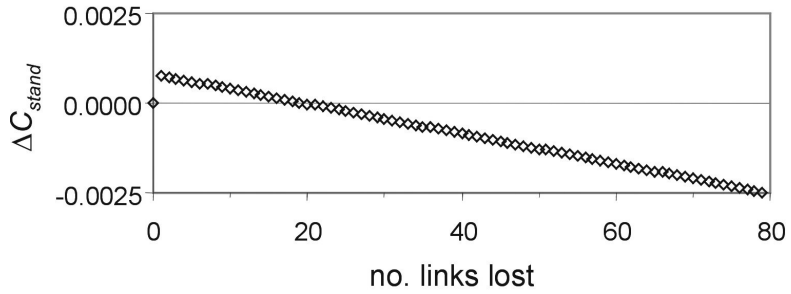


Figure 5.8 Change in standardised, directed connectance with the loss of one species for 0 to 80 links; the original network comprises 156 species, 1518 links, and has an initial connectance of 0.0560

More than one species may be lost from a food web. Figure 5.9 repeats Figure 5.8, considering the loss of one, two and three species.

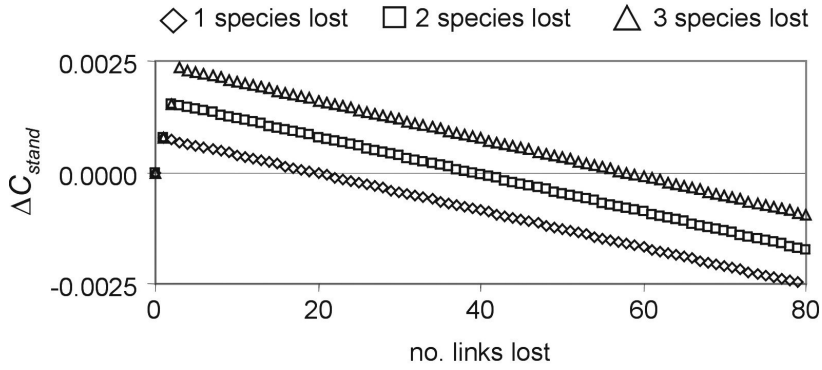


Figure 5.9 Change in standardised, directed connectance with the loss of 1, 2 and 3 species, each for 0 to 80 links; the original network comprises 156 species, 1518 links, and has an initial connectance of 0.0560

Figure 5.8 and 5.9 show that the loss of species with relatively few links leads to a positive change, while the loss of species with many links leads to a negative change in connectance. I term the intercept on the *x*-axis, where the change to connectance switches from positive to negative, the breakpoint. For one species lost, the breakpoint occurs between 19 and 20 links. Because the breakpoint is not an integer, the loss of a species will nearly always lead to a change to connectance.

This general pattern of change – small positive changes for poorly-connected and large negative changes for highly-connected species – is the same for all realistic combinations of species and links. The pattern, and the breakpoint, can be generalised to any

combination of S and L. The number of links that may be lost without change to connectance is derived as follows.

$$\Delta C = \frac{L}{S^2} - \frac{(L-\Delta l)}{(S-\Delta s)^2} = 0$$

$$0 = L(S-\Delta s)^2 - (L-\Delta l)S^2$$

$$L - \Delta l = \frac{L(S-\Delta s)^2}{S^2}$$

$$\Delta l = L\left(1 - \frac{(S-\Delta s)^2}{S^2}\right) \qquad \text{Eq. 5.4}$$

where

Δl = breakpoint, or the number of links lost for no change to connectance; and,

Δs = number of species lost.

Equation 5.4 shows that the breakpoint is a function of the number of species lost, Δs, and is always positive. Breakpoints are multiples, approximately, of the average number of links per species:

$$\Delta l = L\left(1 - \frac{(S-\Delta s)^2}{S^2}\right)$$

$$= L\left(1 - \frac{\left(S^2 - 2S\Delta s + \Delta s^2\right)}{S^2}\right)$$

$$= L\left(\frac{2S\Delta s - \Delta s^2}{S^2}\right)$$

$$= \Delta s \frac{L}{S}\left(\frac{2S - \Delta s}{S}\right)$$

$$\approx 2\Delta s \frac{L}{S} \qquad \text{for small } \Delta s \qquad \text{Eq. 5.5,}$$

The average number of links per species for the web used in Figures 5.8 and 5.9 is 9.7. The breakpoints in Figure 5.9 are 19.4, 38.7 and 57.8 for the loss of 1, 2 and 3 species respectively, and correspond to, approximately, two, four and six times the average number of links per species.

The loss of a species from a network can trigger an increase or decrease in connectance. The loss of fewer links than the breakpoint causes connectance to increase, and the loss of more links causes connectance to decrease. Dunne *et al*. (2002b) showed that food webs with a higher connectance displayed greater robustness. If a food web loses poorly-connected species, and its connectance increases, does this correspond to an increase in robustness? Does the converse hold, that the loss of highly-connected species and a decline in connectance correspond to a decrease in robustness? These questions are addressed in Section 5.4.

5.3.3 Gain of species

The addition of species, just as with their loss, also causes positive and negative change to connectance, as shown in Figure 5.10. The trend is reversed: adding poorly connected species decreases, while adding highly connected species increases connectance.

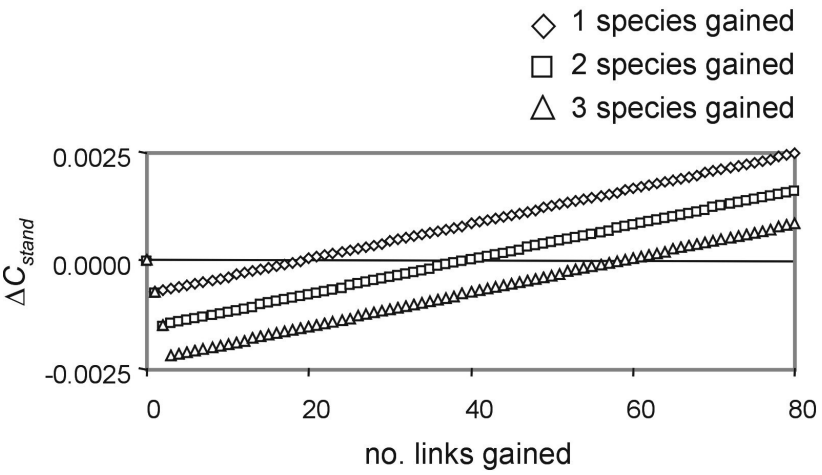


Figure 5.10 Change in standardised, directed connectance with the gain of 1, 2 and 3 species, each for 0 to 80 links; the original network comprises 156 species, 1518 links, and has an initial connectance of 0.0560

For a network of S species with L links, the number of links that can be added without change to connectance (i.e. the breakpoint) is derived by:

$$\begin{aligned} \Delta C &= \frac{L}{S^2} - \frac{(L+\Delta l)}{(S+\Delta s)^2} = 0 \\ 0 &= L(S+\Delta s)^2 - (L+\Delta l)S^2 \\ L+\Delta l &= \frac{L(S+\Delta s)^2}{S^2} \\ \Delta l &= L\left(\frac{(S+\Delta s)^2}{S^2} - 1\right) \end{aligned} \qquad \text{Eq. 5.6}$$

where

Δl = breakpoint, or the number of links lost for no change to connectance; and,

Δs = number of species gained.

Again the breakpoint is always a positive number ($S+\Delta s > S$), as well as a multiple, approximately, of the average number of links per species:

$$\begin{aligned} \Delta l &= L\left(\frac{(S+\Delta s)^2}{S^2} - 1\right) \\ &= L\left(\frac{S^2 + 2S\Delta s + \Delta s^2}{S^2} - 1\right) \\ &= \Delta s \frac{L}{S}\left(\frac{2S+\Delta s}{S}\right) \\ &\approx 2s\frac{L}{S} \end{aligned} \qquad \text{for small } s \qquad \text{Eq.5.7}$$

The breakpoints for addition of 1, 2 and 3 species are 19.5, 38.8 and 58.0 respectively (see Figure 5.10). While still approximately two, four and six times the average number of links per species, the breakpoints for species gain and for species loss are different.

If a species entering a food web links with few species in the existing network, connectance decreases; if it links with many, connectance increases. The number of possibilities of species additions and links made to existing food web is very large. Intuitively, not all of these possibilities are likely, and the likely possibilities are probably a function of the dynamics of species interactions – in particular competition, but certainly more than just consumption – that are not treated in this analysis. The following discussion considers possible effects of species addition on connectance as suggested by the literature.

5.3.4 Growth of food webs

Two perspectives on the addition of nodes to networks can be found in the literature (see Chapter 4). The first relates to preferential attachment. Barabási and Albert (1999) demonstrated that a power-law degree distribution emerged from a stochastic growth model in which new nodes were added continuously, attaching themselves preferentially to highly-connected nodes. Connectance can provide no information on preferential attachment. Should a new species form a link to an existing food web, the change to connectance is the same whether the link is made to a poorly- or a highly-connected species.

Introduced and invasive species have been used to ponder whether preferential attachment occurs when species enter new communities (see Chapter 4). The transition from merely introduced (present but not to any large or influential extent) to invasive is not well understood (see Chapter 2). However its effects – species extinction and change to habitat – strongly suggest fragmentation of ecological networks as the invasive species redirect matters and energy flows to support its own biomass.

The second perspective relates to the emergence of hubs, as reported by Jain and Krishna (2002). These authors showed that the emergence of new hubs could have an effect similar to hub loss, viz. secondary extinction and network fragmentation. Connectance can provide information on the immediate new state of the network and the template on which further ecological development and coevolution will be based. Secondary extinctions and network fragmentation could stem from, for example:

- competition for resources leading to competitive exclusion;
- the new hub could drive some prey populations down to extinction;
- the combination of points 1) and 2) could be the loss of a relatively balanced set of weak and strong links, some of which could be redundant, with a smaller number of very strong links, and so destabilised the network (see Chapter 2); and,
- the new hub redirects matter and energy flows towards itself, leaving some species, even sub-networks of species, without sufficient resources.

It is possible that the shift from introduced to invasive species coincides with the emergence of a new hub. However some, perhaps many, invasive species thrive because they have no predators – there are no ‘top-down’ controls. Hubs in food webs are more likely to be intermediate consumers with both prey and predators. Links in both directions would increase the maximum possible number of links. The most highly-connected species in the two webs discussed in subsequent sections were intermediate consumers.

An echo of the notion that new highly-connected species can cause extinctions may also be found in Solé *et al*. (2002). These authors argue for a negative feedback, mediated by connectance, between diversity and extinction (see Figure 5.11). My analysis above shows that an increase in diversity does not necessarily bring about an increase in connectance. The feedback mechanism in Figure 5.11 would only operate with the entry of species that form multiple connections, and ultimately become well-connected.

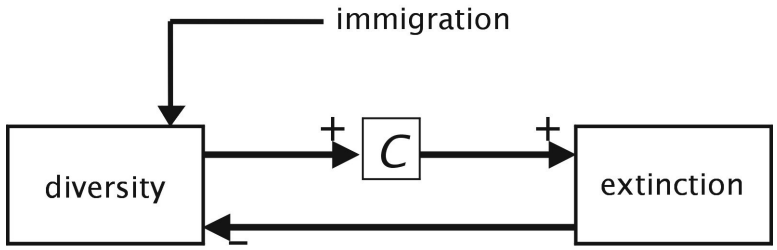


Figure 5.11 Feedback between diversity and extinction mediated by connectance (Solé et al. *2002)*

Secondary extinction and fragmentation indicate reduced robustness. Just as the trend in Figure 5.10 is the opposite of that in Figure 5.9, the effects connectance changes could also be reversed. Sharp increases in connectance have potentially large impacts on robustness. It is not clear whether the addition of poorly-connected species, with a small decline in connectance, also leads to reduced robustness.

5.4 Connectance change with species loss

5.4.1 Introduction

The skewed degree distributions found in real world networks mean that the majority of nodes are poorly connected and only a few are highly connected. Such distributions are believed to lie behind robustness to random node loss and fragility to targeted loss of hubs, as discussed in Chapter 4. The response of food webs to species loss has recently been studied, notably by Solé and Montoya (2001) and Dunne *et al*. (2002b). Their results showed that food webs displayed a similar response to species loss as other real world networks. Dunne *et al*. also showed that food webs with a higher connectance were more robust, or less fragile, to targeted attack on hubs.

My interest in node loss stems from the social impact on natural ecosystems, summarised in Chapter 2. The general effect of social impact is loss of biodiversity. There are fears that this could compromise the stability of ecosystems. The following analysis aims to generalise the relationship between connectance and robustness when species are lost from food webs. It repeats species removal sequences for two of the 16 food webs analysed by Dunne *et al*. (2002a and b). Rather than using connectance as a measure for comparison across food webs, I assess whether connectance provides information about how a given ecological community might be affected by species loss. Three removal sequences are simulated on two food webs. The procedure for species removals is outlined in Section 5.4.2, and the results are presented in Sections 5.4.4-5.4.6.

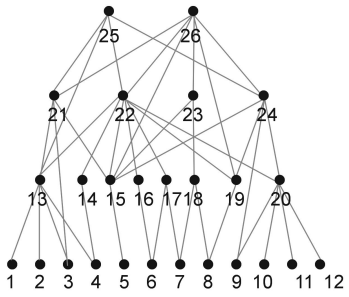
5.4.2 Procedure for species removal

Feeding data for two food webs from the literature, El Verde rainforest and St. Marks seagrass (Dunne *et al*. 2002a and b provide sources), were converted into predation matrices. A predation matrix records community members on rows and columns. A cell entry, a_{ij}, can take the value of 0 or 1. These entries record that species *i* is eaten (1) or is not eaten (0) by species *j*. The predation matrices and species keys for the two food webs may be found in Appendices I-IV.

Removal sequences involve the sequential deletion of rows and columns from the matrices. A species is lost, and so are its links to predators and prey. After a species is removed, the matrices are checked for fragmentation and secondary extinctions. Secondary extinctions are indicated by the loss of all sources of prey and/or no links to other species in the network (e.g. a plant that is no longer eaten). Fragmentation requires careful checking of the matrix. One indication of fragmentation is a number of links fewer than *S*-1, the minimum number of links for an intact network of *S* species (see Section 5.2). The difference between secondary extinction and fragmentation is illustrated in Box 5.1. Small-scale fragmentation is easy to detect. Large-scale fragmentation is not, and despite careful checking, it may have been missed in the simulations below.

Box 5.1 Secondary extinction and fragmentation

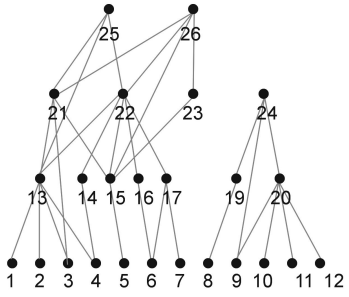
The network above at right represents a simple, hypothetical food web. Lines connecting the 26 species indicate a feeding relationship. The food web comprises four trophic levels. Species 25 and 26 are top predators, and species 1 to 12 are basal (plant) species. In between these extremes are two trophic levels comprising intermediate consumers.



Species 15 depends on only one source of food. The removal of species 5 deprives species 15 of sustenance and so it will become secondarily extinct. This assumes that species 15 cannot switch to alternative sources of food. Loss of species 15 does not trigger other secondary extinctions.

Alternatively, if species 15 were removed, species 5 would no longer be linked to the network. This is small-scale fragmentation. Species 5 could continue to exist in the absence of consumption, but is not connected to the network.

Large-scale network fragmentation is illustrated in the second figure. Here links and species have been lost in such a way that the network has split into two unconnected subnetworks.



Rows and columns for the secondarily lost or fragmented species are then deleted. In a small number of cases this led to a cascading loss of species. Once all secondarily lost

species are removed, (standardised, directed) connectance is recorded, and the next species removed. Removals continue until approximately 50% of species are lost.

The first removal protocol removes highly-connected species. Species were ranked according to their number of links to both predators and prey, and the highly-connected species were removed beginning with the most connected. Results are discussed in Section 5.4.3. Appendices V and VI of this chapter shows the 25% most connected species from both webs, and indicate the trophic level of each species. Highly-connected species tend to be intermediate consumers.

The second protocol follows the same procedure but removes the least-connected species (Section 5.4.4). The loss of poorly-connected species leads to an increase in connectance. Dunne *et al*. (2002b) showed that food webs with a greater connectance were also more robust. Could this increase correspond to an increase in robustness? This question is addressed in a further set of removals. Removed species switch from least- to most connected-species after a given proportion of species (5, 10, 15, 20, 30 and 40%) had been lost.

The third protocol removes species randomly (Section 5.4.5). The results of these removal sequences are presented as plots of standardised connectance versus species lost, and as indexed connectance versus species lost. Indexing shows the proportionate effects on connectance of species loss, and allows comparison of the two food webs.

There are a number of constraints to this procedure. Firstly, more factors are involved in robustness than just network topology. Predation matrices show the presence or absence of a feeding interaction, but provide no indication of the strength of that interaction. It is to be expected that the effect on food webs of losing strong interactions will be different from that of losing weak interactions. Secondly, examination of network topology does not consider important dynamics that would, for example, enable species to survive by switching to less preferred prey. Finally, the procedure does not consider the possibility of strong non-trophic interactions and indirect effects. For example a species with a powerful influence on habitat may not be highly-connected within feeding networks. Its loss may trigger secondary extinctions that are not related to feeding.

5.4.3 Removal of the most-connected species

Figure 5.12a shows that removal of the most connected species led to a sharp decrease in connectance. The initially sharp decline levels off as less highly-connected species are removed. The slight increase in the seagrass food web when more than 40% of species have been lost indicates that the number of links being lost is less than the breakpoint. Figure 5.12b shows that the impact on connectance for the rainforest is greater than for the seagrass food web. Both webs suffer secondary extinctions. The rainforest web lost a species secondarily with removal of the most-connected species; the seagrass lost its first species secondarily after the ninth species was removed. The rainforest web lost 28 species (18%) and the seagrass 7 (14.5%) secondarily. The difference in secondary losses between the two webs is unlikely to be significant. Secondary losses can be seen in Figure 5.9 as larger gaps between data points. These gaps coincide with a reduced decline, even increase, in connectance. Secondarily lost species are generally poorly-connected, and so their impact on connectance is relatively mild.

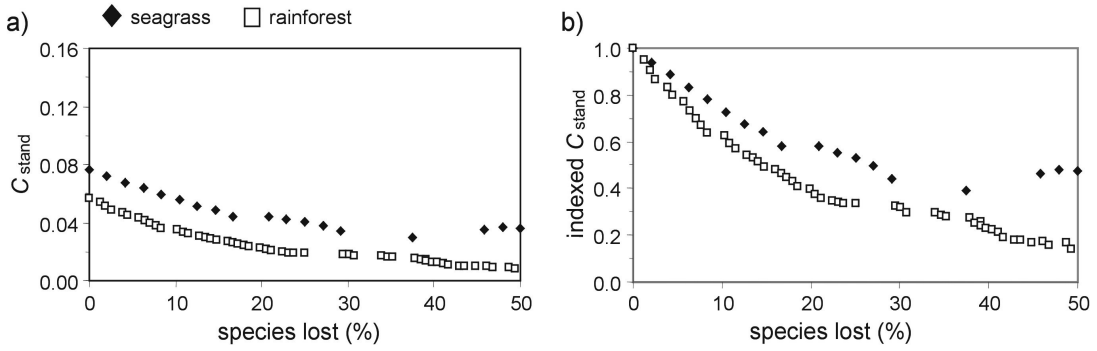


Figure 5.12 Change in connectance with removal of the most connected species for two food webs, St. Marks seagrass and El Verde rainforest

Figure 5.13 shows the rank of species lost secondarily. Species were ranked from most to least connected; the most-connected was assigned a rank of 1, and the least a rank of 156 (rainforest) and 49 (seagrass). The dashed line in Figure 5.13 divides species into two halves: highly-connected (under the line) and poorly (above the line). The plots clearly show that secondarily lost species were poorly-, at best moderately-connected.

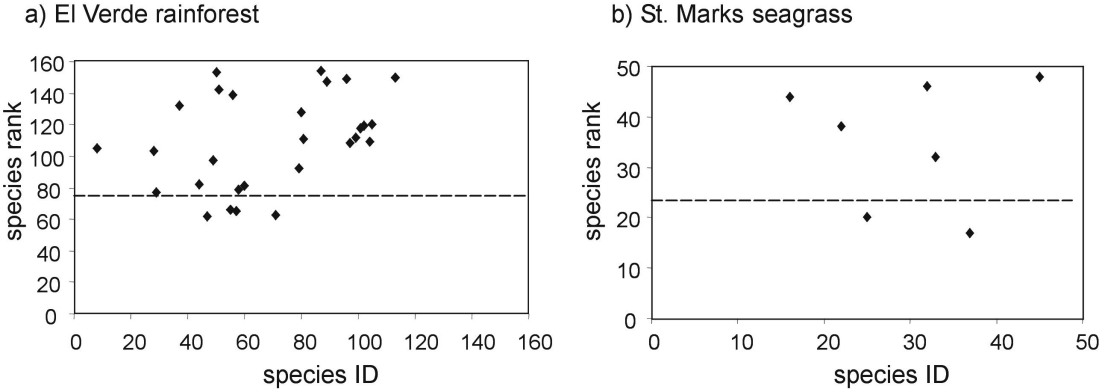


Figure 5.13 Scatter diagram showing species rank (i.e. how connected, with the most highly-connected species having a rank of 1) plotted against species ID; dashed line separates the more-connected half from the less-connected half

My analysis shows that the seagrass food web, with its higher connectance, is the more robust against loss of highly-connected species. Figure 5.12 suggests that this relative robustness also manifests itself as a less abrupt decline in connectance with species loss. A decline in connectance with species loss corresponds to reduced robustness (or increased fragility); the greater the decline, the greater the impact on robustness.

5.4.4 Removal of the least connected

Figure 5.14 presents the results from removing the least connected species. Connectance increases, perhaps more strongly for the rainforest. Secondary losses of species are much fewer than when the most-connected were removed. Both webs lose 2 species secondarily. The rank of these species is 23 and 27 (of 156 species) for the rainforest, and 12 and 21 (of 48 species) for the seagrass. In contrast to the pattern in Figure 5.13, secondarily lost species for this removal sequence are relatively well-connected.

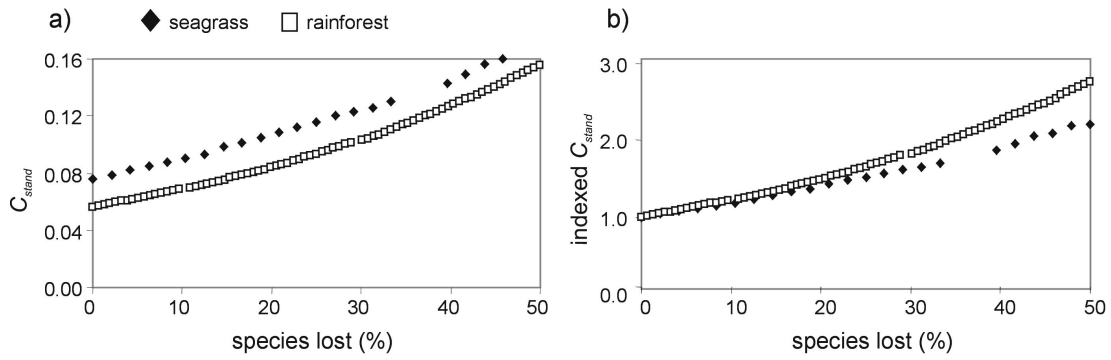


Figure 5.14 Change in connectance with removal of the least connected species for two food webs, St. Marks seagrass and El Verde rainforest

Dunne *et al*. (2002b) showed that food webs with a greater connectance were more robust. Whether the increase in connectance, brought about by the loss of poorly connected species, corresponds to an increase in robustness is addressed by an additional sequence of removals. Least-connected species were removed until a specified percentage of species had been lost: 5%, 10%, 15%, 20%, 30% and 40% species. The removal sequence then switched to the most connected species. The results are presented in Figure 5.15.

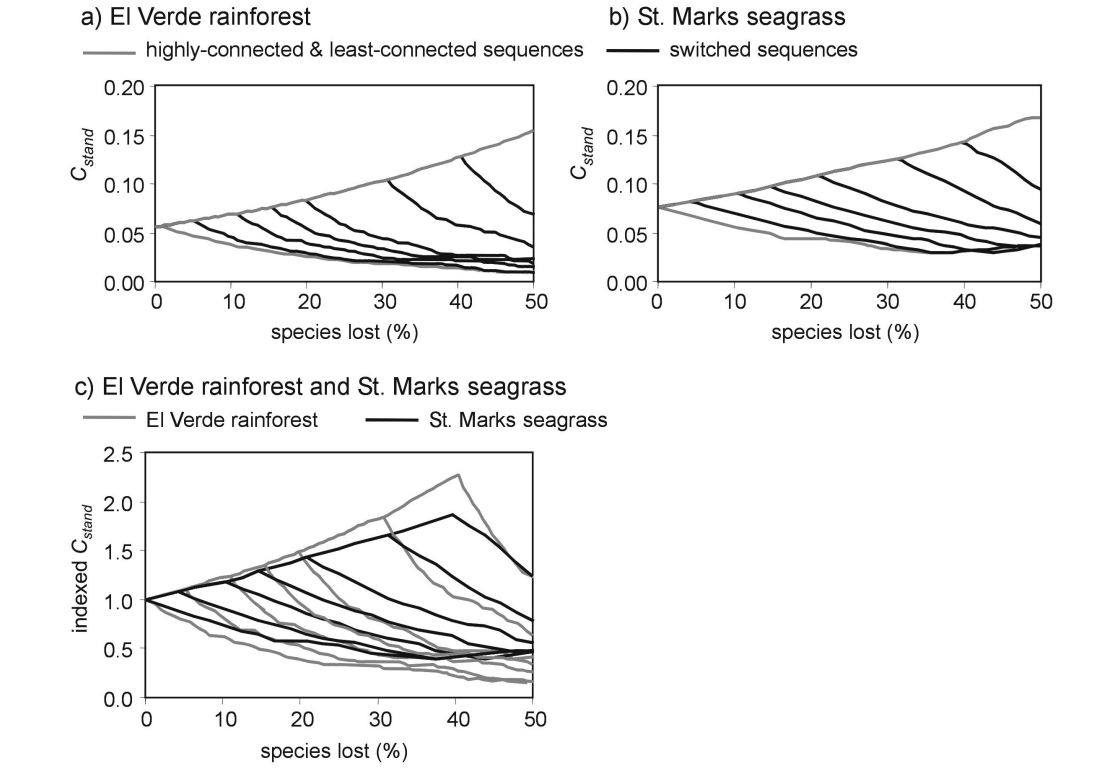


Figure 5.15 Change in standardised connectance with a switch from removing poorly connected to highly connected species after 5%, 10%, 15% 20%, 30% and 40% loss of species; a) rainforest, b) seagrass, c) indexed for both webs

Figures 5.15a and b show standardised directed connectance for the rainforest and the seagrass respectively. Lines joining points are used for better distinction of the different removal sequences. The plots include, for comparison, the sequences removing the most-

connected and the least-connected species. These have the lighter line colour. Figure 5.15c compares the responses of the two webs with connectances indexed.

The switch from least- to most-connected species triggers an abrupt shift from increasing to decreasing connectance. The trajectories for the rainforest are steeper than those for the seagrass. The impact on the rainforest would seem to be greater. The slope of the trajectories becomes steeper as more species are lost before the switch. Loss of poorly-connected species could be decreasing robustness. This is examined in two ways.

Firstly a student's *t*-test is used to test for statistical differences between slopes of the trajectories in Figure 5.15a and b. The procedure for comparing slopes is described in Steel and Torrie (1981) and the results are presented in Table 5.2. Lines were fitted to the data points corresponding to the initial loss of 5% species after the switch from least- to most-connected species. The slopes and correlation coefficients of these lines may be found in the second and third columns of Table 5.2. Note that the positive slope comes from regressing connectance on the percent of species remaining, not lost as presented in Figure 5.15. The slope of each trajectory is compared with that for the sequence that began by removing the most highly-connected species (i.e. the light grey trajectories to the extreme left of Figures 5.15a and b), generating the *t*-statistic in the fifth column. A two-sided probability for the *t* value is determined for n_1-2+n_2-2 degrees of freedom and is given in the last column. No significant difference between slopes is taken to be indicated by a probability greater than 0.05. Such a probability, with the conclusion that the slopes are the same, occur in only one comparison, highlighted in Table 5.2.

Table 5.2 Results from the statistical comparison of slopes as connectance declines following a switch from removing the least- to the most-connected species

Sequence*	Slope (*b*)	Correlation coefficient (r^2)	Comparison	*t*-statistic	2-sided probability
R0	0.041	0.975			
R5	0.056	0.974	R5 with R0	3.36	0.00633
R10	0.076	0.994	R10 with R0	9.82	0.000000436
R15	0.082	0.994	R15 with R0	11.24	0.000000100
R20	0.089	0.995	R20 with R0	15.66	0.00000000237
R30	0.110	0.995	R30 with R0	20.26	0.000000000120
R40	0.129	0.995	R40 with R0	19.53	0.000000000184
S0	0.026	0.999			
S5	0.028	0.999	**S5 with S0**	2.14	**0.0991**
S10	0.032	0.999	S10 with S0	6.44	0.00300
S15	0.034	0.999	S15 with S0	8.95	0.000861
S20	0.040	0.999	S20 with S0	14.80	0.000121
S30	0.047	0.999	S30 with S0	20.76	0.0000318
S40	0.053	1.000	S40 with S0	10.46	0.000473

* R = rainforest; S = seagrass; 0, 5, 10, 15, 20, 30, and 40 = percentage of species lost before switch to most-connected

Table 5.2 shows that there are significant differences between all (except one) trajectories when compared with the base trajectory. The exception shows that the decline in connectance after 5% loss from the seagrass food web is not significantly different from the decline when species removal begins with the most-connected species. The robust-

ness of this web is affected only when between 5 and 10% of the least-connected species have been removed. The probability that slopes are the same generally decrease as more species are lost before the switch. The significant differences between slopes mean that the decline in connectance is greater when species have already been lost, and so that the increase in connectance has led to decreased robustness.

This conclusion is supported by a second analysis. Robustness is defined in terms of the number of species lost secondarily. Table 5.3 examines secondarily lost species.

Table 5.3 Secondarily lost species from the switched removal sequences

ID of species lost secondarily	Percentage of species lost before switch to most-connected**					
- most-connected sequence*	5	10	15	20	30	40
El Verde rainforest						
113	L-C	L-C	L-C	L-C	L-C	L-C
51		L-C	L-C	L-C	L-C	L-C
87	L-C	L-C	L-C	L-C	L-C	L-C
37& 49			L-C	L-C	L-C	L-C L-C
71					***82***	L-C
29						
80				L-C	L-C	
58						
50	L-C	L-C	L-C	L-C		
97&99&101&102&104&105						
55&57&60&81						
47&96, 89	L-C	L-C ***32***	L-C			
44		***48***				
79						
8&28						
56						
St. Marks seagrass						
32	L-C	L-C	L-C	L-C	L-C	L-C
37,33, 45	L-C	L-C	L-C	L-C ***42***		
16& 22&25			L-C ***42***			

* species IDs separated by an ampersand mean that species were lost simultaneously; IDs separated by a comma mean that species were lost sequentially (i.e. cascading loss).

** L-C: species lost during removal of the least connected species and prior to the switch; shading indicates >50% of species lost and removals terminated; ID nos. - additional species lost /change in the order of secondary loss

The first column of Table 5.3 lists the identification (ID) numbers of species lost with removal of the most-connected species. Subsequent columns indicate changes to this pattern. Species removals terminated when about 50% of species had been lost. The grey cells indicate that this limit had been met and no further species were removed. A number of species have already been lost prior to the switch, with the removal of least-connected species. These are indicated. That loss of the least-connected species adversely affected robustness is indicated by additional loss of species (numbers in bold and italic), and by the earlier loss of species secondarily. Additional species were lost secondarily for both webs: species 32, 48 and 82 for the rainforest, and species 42 for the seagrass. Species 42 is lost earlier.

My conclusion is that the increase in connectance with the loss of poorly-connected species reduces robustness. Reduced robustness is manifest before 5% of species have been lost from the rainforest food web, and between 5 and 10% for the seagrass. The seagrass food web is, again, more robust to species loss.

5.4.5 Random removals

Figure 5.16 and Table 5.4 show the results of removing species randomly. Four removal series were conducted for the seagrass web (data points closed, connected by a line), and two for the rainforest (data points open, not connected).

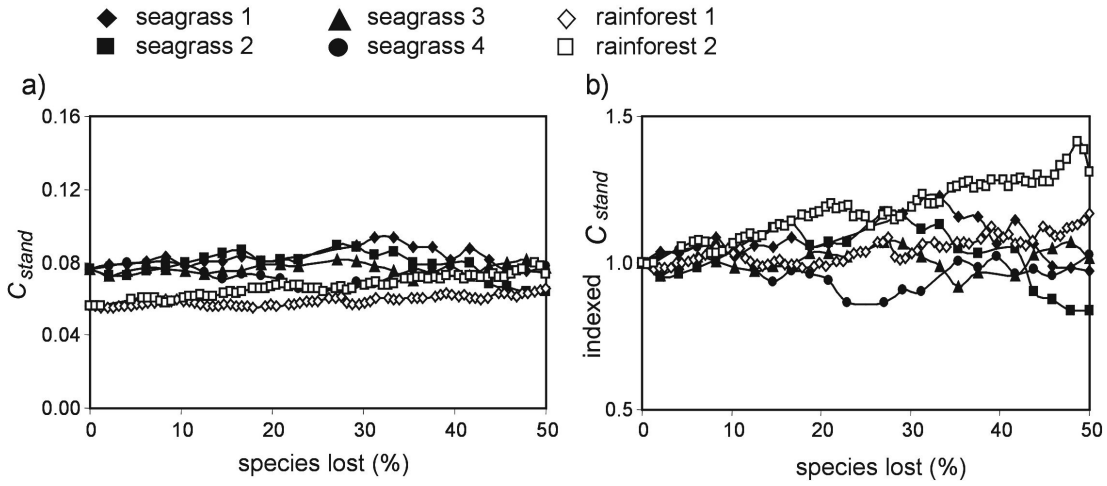


Figure 5.16 Change in connectance with random removal of species from St. Marks seagrass (four sequences) and El Verde rainforest (two sequences) food webs

Figure 5.16 suggests that connectance may increase for the rainforest, but only one of the two sequences shows this clearly. Table 5.4 shows that this second sequence suffered not only more secondary extinctions, but also that the species lost secondarily are poorly-connected. These secondary losses will generated a stronger positive change on connectance for the second in comparison with the first sequence. Figure 5.16 does not suggest a clear trend for the seagrass. It is also difficult to identify a clear trend from the information provided in Table 5.4. The first sequence achieved the highest average connectance, but this cannot be explained by the loss of less-connected species, either for primary or secondary losses. The second and fourth sequences are very similar in terms of the rank of their primary and secondary losses, yet the second achieves a slight increase

in connectance while the fourth a slight decrease. The main difference between these two sequences is that the fourth loses more species secondarily. The third sequence loses less-connected species during the random removals, and none secondarily. The fewer secondary losses with the loss of less-connected species conform to the pattern above (see Section 5.4.4). However its average connectance over the sequence hardly differs from the initial connectance. My tentative conclusion is that random removal of species tends to generate a connectance that oscillates around the initial value of connectance.

Table 5.4 Summary from the random removal of species from the El Verde rainforest (R1 and R2) and St. Marks seagrass (S1, S2, S3 and S4) food webs

	Random removal sequence*					
	R1	R2	S1	S2	S3	S4
Initial C_{stand}	0.0564	0.0564	0.0762	0.0762	0.0762	0.0762
Mean C_{stand}	0.0588	0.0668	0.0822	0.0780	0.0763	0.0740
No. secondary extinctions	7	13	3	2	0	3
(% of species)	(4.5)	(8.3)	(6.3)	(4.2)		(6.3)
Mean rank[1] of primary removals	77.40	77.40	25.67	24.14	27.32	24.33
Mean rank of secondary losses	115.29	136.38	23.33	47.00		45.50

1 Determination of rank follows procedures outlined in sections above.

5.5 Species loss and network topology

5.5.1 Changes to connectance

Sections 5.4 tested the effects on connectance of three sequences for removing species from two food webs. The following trends were observed. Removal of highly-connected species led to a sharp decline, while removal of poorly-connected species led to a gradual increase, in connectance. Sharp declines in connectance are more likely to be followed by secondary species losses. The increase in connectance from removing the least-connected species, while leading to fewer secondary losses, still indicates reduced robustness. Changes to connectance, whether increases or decreases, were generally stronger for the rainforest than the seagrass. I offer four conclusions:

1. large, negative changes to connectance with the removal of highly-connected species lead to the largest, adverse impacts on robustness;
2. the loss of a species from a food web, irrespective of how well connected it is, reduces its robustness;
3. greater robustness to species loss is expressed as smaller changes in connectance with species loss; and,
4. the seagrass is a more robust food web than the rainforest.

Not only did the connectance of the seagrass food web change less than that for the rainforest over all sequences, but also proportionately more poorly-connected species must be removed before robustness is adversely affected (between 0 and 5% of species for the rainforest, versus between 0 and 10% of species for the seagrass).

These conclusions are offered with three caveats. Firstly, only a limited number of removal sequences have been simulated. This is of little consequence for removing the most or least-connected species as the order of species loss is more or less fixed. How-

ever it is difficult to determine trends from random species removal. Secondly, only two food webs are compared. The above analysis needs to be undertaken on more food webs. The third and, in terms of this dissertation, more interesting caveat is that the species removals that have been simulated are unrealistic. There is no *a priori* reason why extinction risk is related to how well species are connected, or that extinction occurs randomly.

The corollary of the second conclusion above is that the loss of species with a number of links that corresponds to the intercept with the *x*-axis (or breakpoint) in Figure 5.9, in that it does not cause a change in connectance, also does affect robustness. There is no apparent logic or ecological reason for this. Removal of such species has been examined, but it is not possible to draw conclusions for two reasons. Firstly, there are no species with exactly this number of links – the number of links is always an integer whereas breakpoints are not, except in rare circumstances. Removal of species with a number of links close to the breakpoint caused slight changes connectance. Secondly, there were only few species with links close to the breakpoint, and too few to observe trends.

5.5.2 A return to degree distributions

Section 5.4 shows that the seagrass was more robust than the rainforest food web. The analysis of Dunne *et al*. (2002b) attributes this to its higher connectance. My analysis shows that the more robust food web displayed limited changes in its connectance with species loss. Could robust food webs be buffered against changes in their topology? To address this question, I return to degree distributions as a measure of topology.

A degree distribution plots the frequency distribution of the number of links per node (P_k) against the number of nodes (k). Figure 4.7 plots the degree distributions of the 16 food webs analysed by Dunne *et al*. (2002 a and b). Such plots are typically log-linear with the number of links plotted against cumulative frequency (Figure 4.7, and see also Amaral *et al*. 2000; Camacho *et al*. 2002); log-log plots may also be used (e.g. Montoya & Solé 2002). Correlations determine the function followed by the degree distribution, such as the power law, exponential and uniform functions indicated in Figure 5.17.

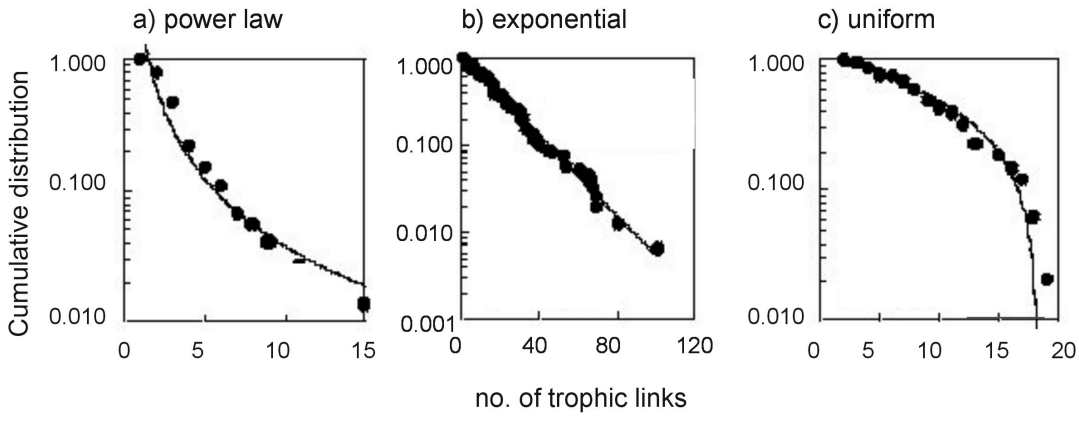


Figure 5.17 Three degree distributions illustrating power law, exponential and uniform functions (adapted from Dunne, et al. *2002a)*

St. Marks seagrass and El Verde rainforest food webs have different degree distributions; the former is uniform and the latter exponential. The degree distributions for these two

webs are shown again in Figure 5.18 but with the *y*-axis showing the percentage of species with a given number of links.

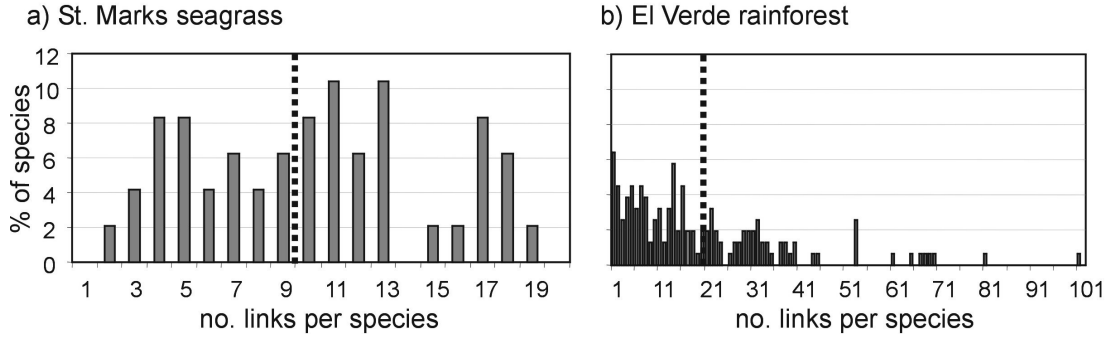


Figure 5.18 Distribution of number of links per species in the El Verde rainforest and St. Marks seagrass food webs

The El Verde rainforest, with its exponential degree distribution has many species with few links and few species with many links. This is definitely not the case with the uniform distribution of the seagrass web ('single-scale' following Amaral *et al.*). Here the distribution is relatively even, or uniform, across categories. The vertical, dotted lines in Figure 5.18 show the breakpoints for the loss of one species (see Section 5.3 and Figure 5.8). The loss of species with fewer links than the breakpoint (to the left of the dotted lines) engenders positive changes, while loss of more links engenders negative changes, to connectance. The different responses of connectance to random and targeted species loss can be explained by these degree distributions and by the position of the breakpoint.

Consider the removal of highly-connected species. The maximum number of links per species for the rainforest is approximately five times the breakpoint; for the seagrass it is about twice as many. The rainforest has a small number of very highly-connected species. The negative impact on connectance brought about by the loss of the most-connected species can be expected to be severer for the rainforest than the seagrass. Section 5.4.3 and, to some extent, Section 5.3.4 showed that this was the case.

Consider the removal of poorly-connected species. The positive change to connectance is greatest for species with only one link. The distributions above show that the rainforest has many very poorly-connected species, but that this is not the case for the seagrass where there are no species with one link and only a few species with two or three links. It can be expected that the increase in connectance with the loss of the least-connected species will be greater for the rainforest than the seagrass, as shown in. Section 5.4..

Consider random removal of species. For the rainforest, 62% of species have links fewer than the breakpoint and about 10% are highly connected. There is a somewhat greater likelihood of randomly selecting a species that effects a positive change to connectance. A small increase in connectance with the random loss of species can reasonably be expected, and this was the case in the sequences shown in Section 5.4.5. For the seagrass food web, the breakpoint is located in the middle of the degree distribution; 52% of species have a number of links less that the breakpoint. The likelihood of randomly selecting a species with fewer links than the breakpoint is almost the same as the likelihood of selecting one with more links. The uniform distribution also means that the negative effects of removing species with a number of links more than the breakpoint are likely to

be compensated by the positive effects of removing species with a number of links less than the breakpoint. On average, connectance can be expected to change little with random species removals. Section 5.4.5 showed that this was the case.

Dunne *et al*. (2000b) related robustness with connectance. This discussion suggests two additional factors – degree distribution and the position of the breakpoint – that lie behind patterns of robustness. The latter, like connectance, is a function of the number of species and links, and so is an aggregated measure of topology. Of the 16 webs investigated by Dunne *et al*., those with the highest connectances tended to display uniform degree distributions. Figure 5.19 repeats Figure 4.7 but adds the breakpoints for one species lost. See also Table 5.5.

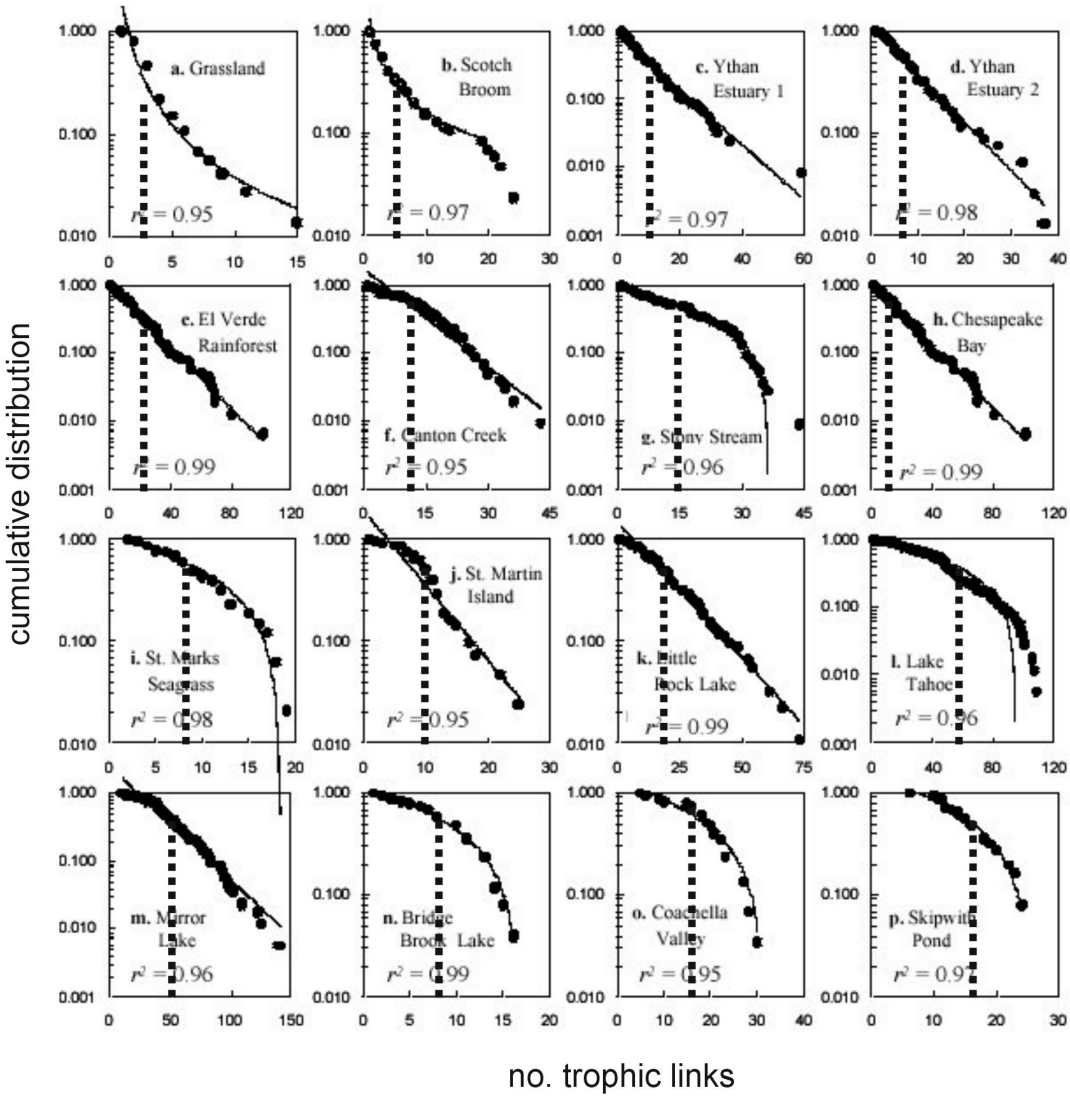


Figure 5.19 Location of breakpoints for one species lost (dotted, vertical lines) in the degree distributions of 16 food webs (adapted from Dunne et al. *2002a)*

A downward turning fit indicates a uniform distribution. Webs with uniform degree distributions (i.e. Stony Stream, Lake Tahoe, Bridge Brook Lake, Coachella Valley and Skipwith Pond and St. Marks seagrass) share the two features that, as my analysis shows, support robustness, viz.:

- a uniform degree distribution where the proportions of species with different numbers of links are approximately the same, and,
- an intermediate breakpoint.

The remaining webs display a skewed distribution with many poorly-connected species and few very highly-connected species. The breakpoints are less central, and located more to the left of the degree distributions.

Table 5.5 Breakpoints for the loss of one species from 16 food webs

Food Web	*S*	*L*	Breakpoint
Grassland	61	96	3.1
Scotch Broom	85	222	5.2
Ythan Estuary 1	124	579	9.3.
Ythan Estuary 2	83	395	9.5
El Verde Rainforest	155	1509	19.4.
Canton Creek	102	696	13.6
Stony Stream	109	829	15.1.
Chesapeake Bay	31	67	4.3
St. Marks Seagrass	48	220	9.11
St. Martin Island	42	204	9.6
Little Rock Lake	92	997	21.6
Lake Tahoe	172	3885	45.0.
Mirror Lake	172	4322	50.1.
Bridge Brook Lake	25	107	8.4
Coachella Valley	29	261	17.7
Skipwith Pond	25	197	15.4.

My analysis leads to two conclusions. Firstly, food webs with a uniform degree distribution are better placed to limit changes to their connectance with species loss. Secondly, robustness is not only a function of connectance, but also of degree distribution and so of the structure of the food web. Connectance captures only a highly aggregated property of a food web. Robustness also depends on deeper properties.

5.6 Conclusions

5.6.1 Summary

This chapter addressed three aims. The first was to examine the behaviour of connectance as a measure of a system's connectedness. Connectance records the proportion of possible links among components that are realised. Three different ways of calculating this proportion have been proposed, but only two – interactive and directed connectance – were examined. The third, upper connectance, attempts to include competitive interactions but its assumption on how to do this may not hold. Martinez (1991) showed that directed connectance was the most robust measure of connectedness when confronted with different levels of resolution of food web data. My analysis supports Martinez in his

preference for directed connectance, by showing that directed connectance behaved more consistently than interactive connectance for relatively small networks.

For large networks, connectance may be assumed to vary smoothly between 0 and 1. For small networks, the minimum value of connectance is not 0, and connectance takes on discrete values between this minimum and 1. The transition between small and large networks occurs around 50 nodes for directed connectance, and around 100 nodes for interactive connectance.

Many food webs studied by ecologists comprise less than 50 species. For example, none of the 113 webs detailed in Cohen *et al*. (1990) are larger than 50 species. Difficulties with studying small food webs are generally recognised by ecologists. My analysis adds to concerns with very small food webs, viz. those smaller than about 20 species. I also raises concerns with the comparison of food webs, particularly when one or more are small. Connectance requires standardisation, spreading values between 0 and 1, before meaningful comparisons can be made. The potential importance of standardisation for ensuring consistent interpretations is indicated by my recalculation of the connectances of 16 food webs analysed by Dunne *et al*. (2002b).

My second objective was to generalise the relationship between connectance and changes in the number of species in a food web. Small and positive changes to connectance occur with the loss of poorly-connected species; the change is large and negative when highly-connected species are lost. The converse holds for species gain. The addition of a poorly-connected species causes a small negative change to connectance, and potentially a large positive change if highly-connected. The breakpoint – the number of species and links lost or gained that would cause no change to connectance – can be calculated. Since the number of links is always an integer, it is only very rare that the loss or gain of species will engender no change in connectance.

My third objective was to relate robustness and network topology with species removal from a food web. I tracked changes to connectance with the removal of species from the El Verde rainforest and St. Marks seagrass food webs. Large, negative changes to connectance, with the removal of highly-connected species, led to the largest, adverse impacts on robustness. However the loss of species from a food web, irrespective of how well connected it was, reduced the webs' robustness. Thresholds would seem to be involved in this effect, so that some food webs may be able to lose more species before robustness is adversely affected. Greater robustness to species loss was expressed as smaller changes in connectance with species loss. Finally, all of my removal sequences confirmed that the seagrass food web was more robust than the rainforest food web.

Connectance is an aggregate measure of connectedness, capturing the number, but not the pattern or structure of links among species. Other measures of pattern found in the literature include characteristic path length, clustering (see Box 4.4) and degree distribution (see Chapter 4). The analysis of food web patterns performed by Dunne *et al*. (2002a) showed few consistent trends across 16 food webs with regards to path length and clustering. However, a loose relationship between degree distribution and connectance can be inferred. Food webs with a higher connectance tended to display a uniform distribution. Food webs with a low connectance did not display this form of degree distribution.

I returned to webs' degree distributions to examine more closely why the seagrass food web is the more robust, and showed that food webs with a uniform degree distribution, and also with an intermediate (one species lost) breakpoint, are better placed to limit changes to their connectance with species loss. Robustness is not only a function of connectance, but also of the structure of the food web. Connectance captures only a highly aggregated property of a food web. Robustness also depends on deeper properties.

I offer the following conclusions.

Firstly, the loss of species from a food web, irrespective of how well connected they are, reduces a food web's robustness.

Secondly, the impact on robustness is greater the more connected the lost species.

Thirdly, thresholds in impact on robustness can be expected.

Fourthly, greater robustness to species loss is expressed as a smaller change in connectance following species loss.

Fifthly, food webs with a uniform degree distribution are better placed to buffer changes to their connectance with species loss.

Sixthly, robustness is not only a function of connectance but also of the degree distribution and perhaps also other measures capturing the structure or patterns of interactions.

5.6.2 Some speculations

We know from the work of Robert May and subsequent research into food webs, that the pattern of interactions among components of an ecological community is not random, and that it is one factor lying behind ecosystem stability (see Chapter 2). Dunne *et al*. (2002a and b) have added to our understanding of this relationship by examining pattern in food webs and the robustness of food webs with species removal.

Dunne *et al*. have shown that food webs seem to have different patterns of interactions than many real world networks (see also Camacho *et al*. 2002). Does this mean that food webs are fundamentally different from other real world networks, and if so, why? One possible explanation for their different pattern could lie with the mechanisms by which they grow. Neither stochastic growth nor preferential attachment, found by Barabási and Albert (1999) to lie behind power law distributions in model networks, would seem to apply to food webs (see Chapter 4 and Section 5.3.4).

Scale free networks display robustness to random error and fragility to attack on highly-connected nodes. Food web topologies are not only not scale free, but are also more robust, and in particular to attack. Is it possible that interaction patterns within food webs are adaptive? That they have they emerged because they reduce the risk of fragmentation and secondary extinction? Our understanding of coevolution, the long time period over which food webs and ecological communities have existed, and the prevalence of extinction during this time (the number of extinct species is only a little less that the total number that have ever existed) could suggest that food webs tend to self-organise into patterns that reduce secondary extinctions when species are lost. This returns us to the question posed in Section 4.5.4, as a result of the comparison of protein networks and food

webs by Melián and Bascompte (2002). Network topology could reflect the specific challenges that particular networks and systems have met historically.

My analysis showed that changes to connectance adversely affect robustness. This suggests that the pattern of interactions for a given food web, reflected in connectance, represents a relatively robust state for that ecological community. Small changes to the number of links and the number of species reduce this robustness. It is as if this connectance is like an island with some degree of robustness in a sea of increasing fragility as the pattern and connectance changes. It is not just that higher connectances mean more robust. The estimated connectance for any real food web represents a relatively robust state relative, adversely affected by changes in the pattern of interactions.

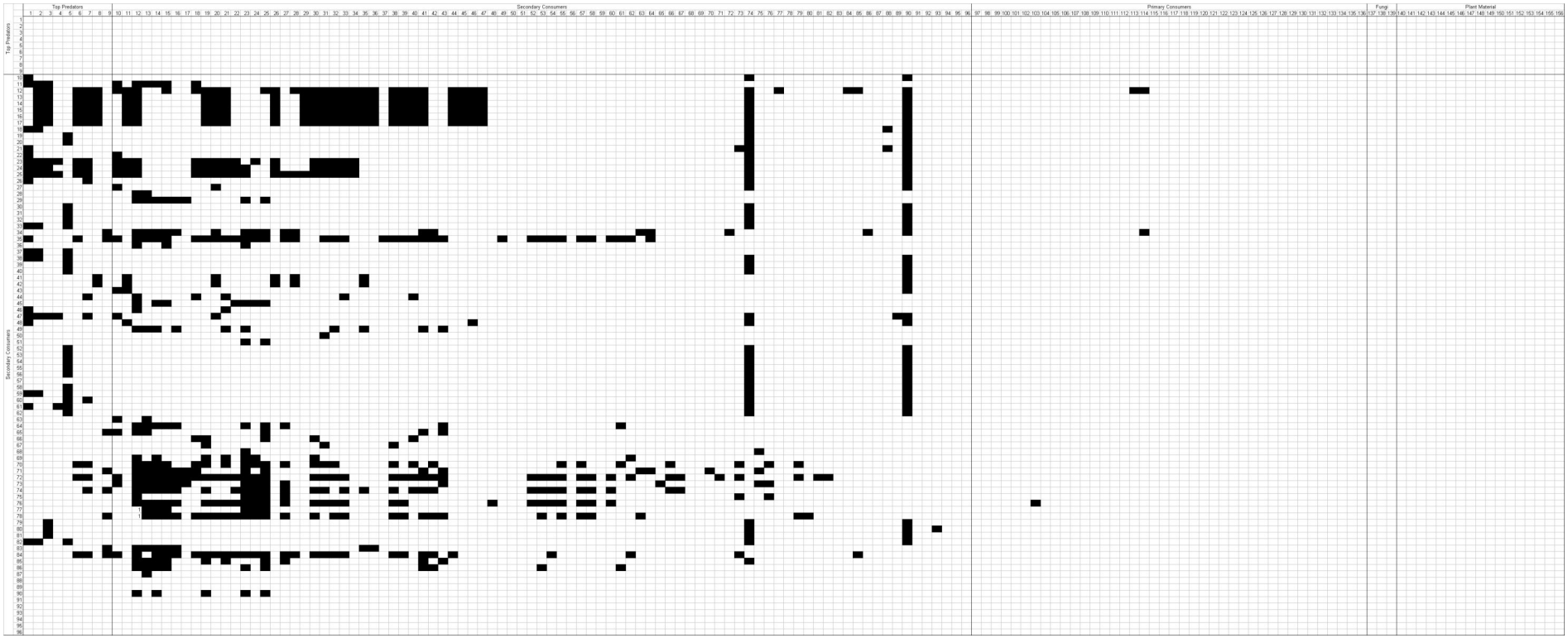
5.6.3 The way forward

The analysis in this chapter has focused on food webs, their topology, their robustness in the light of species loss, and associated changes in connectance. It has shown that robustness declines with species loss, which brings a food web closer to secondary species loss and fragmentation. The hallmark of social impact is loss of biodiversity (see Chapter 2), and so social impact clearly poses a threat to the robustness and, by implication, the stability of ecological communities. Secondary extinctions and fragmentation of ecological networks would fuel biodiversity loss.

I hypothesis that estimated changes to connectance could be used to compare alternative strategies for the management of ecosystems and of the social systems with which they interact. Connectance would indicate the impact of the different strategies on network robustness. However, a number of steps are required before this hypothesis can be tested.

The analysis to date has been focused narrowly, on feeding interactions among ecological networks in isolation from the social systems. Other interactions occur, as discussed in Chapter 3. Components of social systems, their interactions among each other and with components of an ecosystem, also need to be brought into the picture. Finally, the analysis has only addressed species loss from a theoretical perspective that bears little relationship to species actually at risk of extinction from social impact. There is no reason why species should be lost randomly, or that highly- of poorly-connected species are more vulnerable to extinction. Chapter 6 addresses these points.

Appendix I. Predation matrix for the El Verde rainforest food web (blackened cells indicate interaction or a cell entry of ‘1’; unfilled cells indicate no interaction or a cell entry of ‘0’)



Appendix II. Predation matrix for the St. Marks seagrass food web (blackened cells indicate interaction or a cell entry of ‘1’; unfilled cells indicate no interaction or a cell entry of ‘0’)

Appendix III. Species key, El Verde rainforest food web

ID No.	Kingdom	Phylum	Class	Order	Family	Genus	Species	Common Name
1	Animalia	Chordata	Aves	Falconiformes	Accipitridae	*Buteo*	*jamaicensis*	
2	Animalia	Chordata	Aves	Falconiformes	Accipitridae	*Buteo*	*platypterus*	
3	Animalia	Chordata	Reptilia	Squamata	Boidae	*Epicrates*	*inornatus*	
4	Animalia	Chordata	Mammalia	Carnivora	Felidae	*Felis*	*catus*	
5	Animalia	Chordata	Aves	Falconiformes	Accipitridae	*Accipiter*	*striatus*	
6	Animalia	Chordata	Aves	Cuculiformes	Cuculidae	*Saurothera*	*vieilloti*	
7	Animalia	Chordata	Aves	Strigiformes	Strigidae	*Otus*	*nudipes*	
8	Animalia	Chordata	Reptilia	Squamata	Colubridae	*Arrhyton*	*exiguum*	
9	Animalia	Chordata	Reptilia	Squamata	Amphisbaenidae	*Amphisbaena*	*caeca*	
10	Animalia	Chordata	Mammalia	Carnivora	Viverridae	*Herpestes*	*auropunctatus*	
11	Animalia	Arthropoda	Chilopoda	Scolopendromorpha	Scolopendridae	*Scolopendra*	*alternans*	
12	Animalia	Chordata	Amphibia	Anura	Leptodactylidae	*Eleutherodactylus*	*coqui*	
13	Animalia	Chordata	Amphibia	Anura	Leptodactylidae	*Eleutherodactylus*	*richmondi*	
14	Animalia	Chordata	Amphibia	Anura	Leptodactylidae	*Eleutherodactylus*	*portoricensis*	
15	Animalia	Chordata	Amphibia	Anura	Leptodactylidae	*Eleutherodactylus*	*wightmanae*	
16	Animalia	Chordata	Amphibia	Anura	Leptodactylidae	*Eleutherodactylus*	*eneidae*	
17	Animalia	Chordata	Amphibia	Anura	Leptodactylidae	*Eleutherodactylus*	*hedricki*	
18	Animalia	Chordata	Aves	Piciformes	Picidae	*Melanerpes*	*portoricensis*	
19	Animalia	Chordata	Aves	Coraciiformes	Todidae	*Todus*	*mexicanus*	
20	Animalia	Chordata	Aves	Passeriformes	Muscicapidae	*Mimocichla*	*plumbea*	
21	Animalia	Chordata	Aves	Passeriformes	Mimidae	*Margarops*	*fuscatus*	
22	Animalia	Chordata	Reptilia	Squamata	Iguanidae	*Anolis*	*cuvieri*	
23	Animalia	Chordata	Reptilia	Squamata	Iguanidae	*Anolis*	*evermanni*	
24	Animalia	Chordata	Reptilia	Squamata	Iguanidae	*Anolis*	*stratulus*	
25	Animalia	Chordata	Reptilia	Squamata	Iguanidae	*Anolis*	*gundlachi*	
26	Animalia	Chordata	Reptilia	Squamata	Colubridae	*Alsophis*	*portoricensis*	
27	Animalia	Chordata	Amphibia	Anura	Leptodactylidae	*Leptodactylus*	*albilabris*	
28	Animalia	Arthropoda	Arachnida	Amblypygida	Phrynidae	*Phyrnus*	*longipes*	
29	Animalia	Arthropoda	Arachnida	Araneae	Theraphosidae	*Avicularia*	*laeta*	

ID No.	Kingdom	Phylum	Class	Order	Family	Genus	Species	Common Name
30	Animalia	Chordata	Aves	Passeriformes	Tyrannidae	*Myiarchus*	*portoricensis*	
31	Animalia	Chordata	Aves	Passeriformes	Vireonidae	*Vireo*	*latimeri*	
32	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Nesospingus*	*speculiferus*	
33	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Icterus*	*dominicensis*	
34	Animalia	Arthropoda	Arachnida	Acarina	17 families		30 spp.	
35	Animalia	Arthropoda	Arachnida	Araneae	22 families		56 spp.	
36	Animalia	Arthropoda	Arachnida	Araneae	Sparassidae		8 spp.	
37	Animalia	Arthropoda	Arachnida	Araneae	Mimetidae	*Mimetes*	*portoricensis*	
38	Animalia	Chordata	Aves	Passeriformes	Vireonidae	*Vireo*	*altiloquus*	
39	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Seiurus*	*aurocapillus*	
40	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Seiurus*	*motacilla*	
41	Animalia	Chordata	Reptilia	Squamata	Gekkonidae	*Sphaerodactylus*	*klauberi*	
42	Animalia	Chordata	Reptilia	Squamata	Gekkonidae	*Sphaerodactylus*	*macrolepis*	
43	Animalia	Chordata	Reptilia	Squamata	Anginidae	*Diploglossus*	*pleei*	
44	Animalia	Arthropoda	Arachnida	Scorpionida	Buthidae	*Tityus*	*obtusus*	
45	Animalia	Arthropoda	Insecta	Hymenoptera	Formicidae		8 spp.	
46	Animalia	Arthropoda	Crustacea	Decapoda	Pomamonidae	*Epilobocera*	*situatifrons*	
47	Animalia	Chordata	Mammalia	Rodentia	Muridae	*Rattus*	*rattus*	
48	Animalia	Chordata	Amphibia	Anura	Bufonidae	*Bufo*	*marinus*	
49	Animalia	Arthropoda	Chilopoda	Geophilomorpha	2 families		2 spp.	
50	Animalia	Arthropoda	Chilopoda	Scutigeromorpha	Scutigeridae	*Antillora*	*portoricensis*	
51	Animalia	Arthropoda	Insecta	Hymenoptera	Vespidae		2 spp.	
52	Animalia	Chordata	Aves	Apodiformes	Trochilidae	*Chlorostilbon*	*maugeus*	
53	Animalia	Chordata	Aves	Apodiformes	Trochilidae	*Anthracothorax*	*viridis*	
54	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Mniotilta*	*varia*	
55	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Parula*	*americana*	
56	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Dendroica*	*tigrina*	
57	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Dendroica*	*caerulescens*	
58	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Dendroica*	*discolor*	
59	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Dendroica*	*angelae*	
60	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Setophaga*	*ruticilla*	
61	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Coereba*	*flaveola*	
62	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Loxigilla*	*portoricensis*	

ID No.	Kingdom	Phylum	Class	Order	Family	Genus	Species	Common Name
63	Animalia	Chordata	Reptilia	Squamata	Typhlopidae	*Typhlops*	*rostellatus*	
64	Animalia	Arthropoda	Arachnida	Pseudoscorpionida	2 families		2 spp.	
65	Animalia	Arthropoda	Arachnida	Opiliones	3 families		7 spp.	
66	Animalia	Arthropoda	Insecta	Odonata	3 families		12 spp.	
67	Animalia	Arthropoda	Insecta	Mantodea	Mantidae	*Gonatista*	*grisea*	
68	Animalia	Arthropoda	Insecta	Odonata	Coenagrionidae	*Telebasis*	*vulnerata*	
69	Animalia	Arthropoda	Insecta	Neuroptera	5 families		9 spp.	
70	Animalia	Arthropoda	Insecta	Hemiptera	8 families		12 spp.	
71	Animalia	Arthropoda	Insecta	Coleoptera	11 families		32 spp.	(larvae)
72	Animalia	Arthropoda	Insecta	Coleoptera	15 families		33 spp.	
73	Animalia	Arthropoda	Insecta	Diptera	16 families		72 spp.	(larvae)
74	Animalia	Arthropoda	Insecta	Diptera	12 families		158 spp.	
75	Animalia	Arthropoda	Insecta	Hymenoptera	19 families		116 spp.	(larvae)
76	Animalia	Arthropoda	Insecta	Hymenoptera	19 families		109 spp.	
77	Animalia	Arthropoda	Insecta	Hymenoptera	Formicidae		19 spp.	
78	Animalia	Arthropoda	Insecta	Hymenoptera	Formicidae		24 spp.	
79	Animalia	Chordata	Mammalia	Chiroptera	Vespertilionidae	*Eptesicus*	*fuscus*	
80	Animalia	Chordata	Mammalia	Chiroptera	Vespertilionidae	*Lasiurus*	*borealis*	
81	Animalia	Chordata	Mammalia	Chiroptera	Vespertilionidae	*Pteronotus*	*parnelli*	
82	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Spindalis*	*zena*	
83	Animalia	Arthropoda	Arachnida	Schizomida	Schizomidae	*Schizomus*	2 spp.	
84	Animalia	Arthropoda	Insecta	Orthoptera	2 families		23 spp.	
85	Animalia	Arthropoda	Diplopoda		10 families		18 spp.	
86	Animalia	Arthropoda	Insecta	Thysanoptera	2 families		10 spp.	
87	Animalia	Echinodermata	Hirudinea		1 family			
88	Animalia	Arthropoda	Insecta	Diptera	Muscidae	*Philornis*	*sp.*	
89	Animalia	Nemertea	Adenophorea	Trichinellida	Trichuridae	*Capillaria*	*hepatica*	
90	Animalia	Nemertea	Secernentia					nematodes
91	Animalia	Arthropoda	Insecta	Diptera	Streblidae		7 spp.	
92	Animalia	Arthropoda	Insecta	Diptera	Labidocarpidae		5 spp.	
93	Animalia	Arthropoda	Insecta	Diptera	Spinturicidae		4 spp.	
94	Animalia	Arthropoda	Insecta	Diptera	Spelaeorhynchidae		3 spp.	
95	Animalia	Arthropoda	Arachnida	Acarina	Macronyssidae		1 spp.	

ID No.	Kingdom	Phylum	Class	Order	Family	Genus	Species	Common Name
96	Animalia	Arthropoda	Arachnida	Acarina	Argasidae		2 spp.	
97	Animalia	Chordata	Mammalia	Chiroptera	Phylostomidae	*Artibeus*	*jamaicensis*	
98	Animalia	Chordata	Mammalia	Chiroptera	Phylostomidae	*Brachyphylla*	*cavernarum*	
99	Animalia	Chordata	Mammalia	Chiroptera	Phylostomidae	*Erophylla*	*sezekorni*	
100	Animalia	Chordata	Mammalia	Chiroptera	Phylostomidae	*Monophyllus*	*redmani*	
101	Animalia	Chordata	Mammalia	Chiroptera	Phylostomidae	*Stenoderma*	*rufum*	
102	Animalia	Chordata	Aves	Columbiformes	Columbidae	*Columba*	*squamosa*	
103	Animalia	Chordata	Aves	Columbiformes	Columbidae	*Geotrygon*	*montana*	
104	Animalia	Chordata	Aves	Psittaciformes	Psittacidae	*Amazona*	*vittata*	
105	Animalia	Chordata	Aves	Passeriformes	Emberizidae	*Euphonia*	*musica*	
106	Animalia	Arthropoda	Insecta	Hemiptera	5 families		30 spp.	
107	Animalia	Arthropoda	Insecta	Coleoptera	26 families		86 spp.	(larvae)
108	Animalia	Arthropoda	Insecta	Coleoptera	26 families		86 spp.	
109	Animalia	Arthropoda	Insecta	Diptera	6 families		429 spp.	(larvae)
110	Animalia	Arthropoda	Insecta	Diptera	25 families		314 spp.	
111	Animalia	Arthropoda	Insecta	Hymenoptera	6 families		25 spp.	(larvae)
112	Animalia	Arthropoda	Insecta	Hymenoptera	4 families		9 spp.	
113	Animalia	Mollusca	Gastropoda	Stylommatophora	Camaenidae	*Polydontes*	*sp.*	
114	Animalia	Mollusca	Gastropoda	Stylommatophora	Camaenidae	*Caracolus*	*caracolla*	
115	Animalia	Arthropoda	Crustacea	Podocopa				
116	Animalia	Arthropoda	Crustacea	Copepada				
117	Animalia	Arthropoda	Crustacea	Isopoda	Oniscidae	*Philoscia*	*richmondi*	
118	Animalia	Arthropoda	Entognatha	Collembola	4 families		13 spp.	
119	Animalia	Arthropoda	Insecta	Microcoryphia	Machilidae			
120	Animalia	Arthropoda	Insecta	Blattodea	Blattellidae		17 spp.	
121	Animalia	Arthropoda	Insecta	Blattodea	Blattidae		2 spp.	
122	Animalia	Arthropoda	Insecta	Phasmatodea	Phasmatidae		4 spp.	
123	Animalia	Arthropoda	Insecta	Isoptera	2 families		4 spp.	
124	Animalia	Arthropoda	Insecta	Dermaptera	2 families		2 spp.	
125	Animalia	Arthropoda	Insecta	Embioptera	Teratembiidae			
126	Animalia	Arthropoda	Insecta	Psocoptera	9 families		13 spp.	
127	Animalia	Arthropoda	Insecta	Homoptera	15 families		74 spp.	
128	Animalia	Arthropoda	Insecta	Lepidoptera	22 families		234 spp.	(larvae)

ID No.	Kingdom	Phylum	Class	Order	Family	Genus	Species	Common Name
129	Animalia	Arthropoda	Insecta	Lepidoptera	22 families		234 spp.	
130	Animalia	Echhinodermata	Oligochaeta	Haplotaxida	Megascolecidae	*P.*	*hawayana*	
131	Animalia	Arthropoda	Crustacea	Isopoda	Oniscidae		4 spp.	
132	Animalia	Arthropoda	Insecta	Ephemeroptera	Leptophlebiidae		*sp.*	
133	Animalia	Arthropoda	Insecta	Trichoptera	10 families		21 spp.	
134	Animalia	Mollusca	Gastropoda	Stylomatophora	17 families		38 spp.	
135	Animalia	Arthropoda	Insecta	Coleoptera	11 families		15 spp.	(scavenger)
136	Animalia	Arthropoda	Insecta	Coleoptera	8 families		12 spp.	(larvae)
137	Fungi							fungi
138	Fungi							slime moulds
139	Monera							bacteria
140	Plantae							plants
141	Plantae							live leaves
142	Plantae							live wood
143	Plantae							sap
144	Plantae							roots
145	Plantae							pollen
146	Plantae							nectar
147	Plantae							fruits
148	Plantae							seeds
149	Plantae							flowers
150	Plantae							algae
151								lichens
152								dead wood
153								dead leaves
154								SOM
155								dead roots
156								detritus

Appendix IV. Species key, St. Marks seagrass food web

ID No.	Common Name	ID No.	Common Name
1	benthic bacteria	25	pinfish
2	microfauna	26	spot
3	meiofauna	27	pipefish and seahorses
4	bacterioplankton	28	red drum
5	microprotozoa	29	deposit-feeding gastropods
6	epiphyte-grazing amphipods	30	predatory gastropods
7	suspension-feeding molluscs	31	epiphyte-grazing gastropods
8	hermit crabs	32	other gastropods
9	spider crabs (herbivores)	33	deposit-feeding polychaetes
10	omnivorous crabs	34	predatory polychaetes
11	blue crabs	35	suspension-feeding poly-chaetes
12	isopods	36	zooplankton
13	brittle stars	37	benthos-eating birds
14	deposit-feeding peracaridan crustaceans	38	fish-eating birds
15	herbivorous shrimps	39	fish and crustacean-eating birds
16	predatory shrimps	40	gulls
17	catfish and stingrays	41	raptors
18	tonguefish	42	herbivorous ducks
19	gulf flounder and needlefish	43	Halodule wrightii
20	southern hake and sea robins	44	micro-epiphytes
21	atlantic silverside and bay an-chovies	45	macro-epiphytes
22	sheepshead minnow	46	benthic algae
23	killifish	47	phytoplankton
24	gobies and blennies	48	detritus

Appendix V. 25% most connected species, El Verde rainforest

ID	Rank	Species name	No. of Predators	No. of Prey	Total Links	Trophic level[1]
12	1	*Eleutherodactylus coqui*	39	62	100[2]	3
74	2	158 spp. Diptera	29	52	81	3
23	3	*Anolis evermanni*	23	47	70	3
25	4	*A. gundlachi*	26	43	69	3
14	5	*E. portoricensis*	29	39	68	3
13	6	*E. richmondi*	29	38	67	3
15	7	*E. wightmanae*	29	36	65	3
90	8	Nematodes	5	56	61	3
24	9	*Anolis stratulus*	22	31	53	3
16	10	*Eleutherodactylus. eneidae*	29	24	53	3
35	11	55 spp. arachnids	39	14	53	3
108	12	86 spp.Coleoptera	44	9	53	2
72	13	33 spp.Coleoptera	42	3	45	3
135	14	15 spp.scavenging Coleoptera	44	0	44	2
19	15	*Todus mexicanus*	3	37	40	3
21	16	*Margarops fuscatus*	5	35	40	3
128	17	234 spp. Lepidopteran larvae	34	5	39	2
17	18	*Eleutherodactylus hedricki*	29	9	38	3
127	19	24 spp. Homoptera	36	2	38	2
41	20	Sphaerodactylus klauberi	7	30	37	3
76	21	109 spp. Hymenoptera	28	9	37	3
84	22	23 spp. Orthoptera	31	4	35	3
78	23	24 spp. Hymenoptera	30	4	34	3
110	24	314 spp. Diptera	30	4	34	2
70	25	12 spp. Hemiptera	26	7	33	3
112	26	9 spp. Hymenoptera	29	4	33	2
20	27	*Mimocichla plumbea*	3	29	32	3
30	28	*Myiarchus portoricensis*	3	29	32	3
31	29	*Vireo latimeri*	3	29	32	3
147	30	nectar from flowers	32	0	32	1
34	31	30 spp. Acarina	20	11	31	3
106	32	30 spp. Hemiptera	27	4	31	2
129	33	234 spp. Lepidoptera	27	4	31	2
18	34	*Melanerpes portoricensis*	5	25	30	3
33	35	*Icterus dominicensis*	5	25	30	3
148	36	seeds	30	0	30	1
10	37	*Herpestes auropunctatus*	3	26	29	3
32	38	*Icterus dominicensis*	3	26	29	3
38	39	*Vireo altiloquus*	5	24	29	3

1 – 1 = basal species; 2=primary consumer or herbivore; 3=secondary consumer; 4=top predators
2 corrected for cannibalism

Appendix VI. 25% most connected species, St. Marks seagrass

ID	Rank	Species name	No. of Predators	No. of Prey	Total Links	Trophic level
27	1	pipefish and seahorses	10	9	19	2
24	2	gobies and blennies	5	13	18	2
19	3	gulf flounder and needlefish	9	9	18	2
14	4	deposit-feeding peracaridan crustaceans	14	4	17*	2
38	5	fish-eating birds	9	8	17	2
9	6	spider crabs (herbivores)	13	4	17	2
12	7	isopods	16	1	17	2
5	8	microprotozoa	17	0	17	1
15	9	herbivorous shrimps	13	3	16	2
26	10	spot	11	4	15	2
35	11	suspension-feeding polychaetes	4	9	13	2
40	12	gulls	6	7	13	2

1 – 1 = basal species; 2=intermediate consumer; 3=top predators

2 – corrected for cannibalism

6. Social Impact on Ecological Networks

"All tribal myths are true, for a given value of true."

"The Last Continent", Pratchett 1998, p10

6.1 Introduction

Social impact threatens the continued viability of some species. Species loss reduces the robustness of ecological networks, placing them at greater risk of fragmentation and secondary extinction. Chapter 5 showed that the ability of food webs to resist fragmentation and secondary species loss might be linked to the number and pattern of interactions among nodes. However, while Chapter 5 dealt with real world networks, the analysis was not 'real world'.

The goal of this chapter is to make preliminary steps towards applying topological network analysis to environmental management. Topological network analysis assesses the impact of topological changes to a network on that network's robustness. Figure 6.1 illustrates my perspective on how network topology could indicate future directions for the coevolution of social and natural systems. The two systems interact with each other via socio-natural interactions. Social impact, as a result of one or more of these interactions, causes species to be lost from the natural system. These species cannot adapt, or cannot adapt quickly enough, to changing circumstances and so become locally extinct. The robustness of the socio-natural network is adversely affected, leading to fragmentation and secondary losses that may cascade through one or both systems. Fragmentation and secondary losses indicate reduced system connectness, the possibility of a regime shift with new connections among components and a new coevolutionary path.

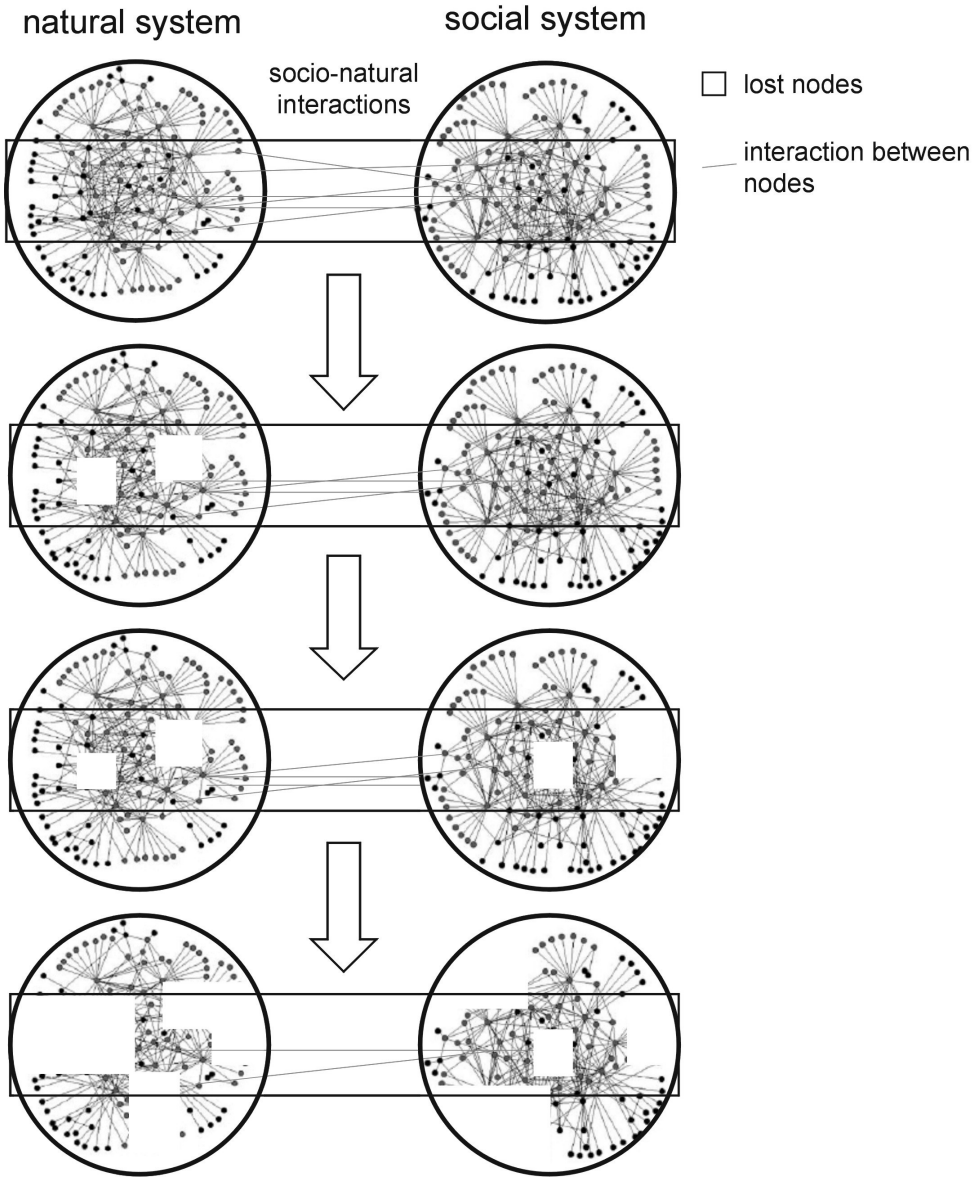


Figure 6.1 Social impact leads to species losses within a natural system, with subsequent secondary losses that may cascade through both systems

I identify four directions for extending the analysis in Chapter 5. The first assesses the ecological character of highly-connected species. The second expands the nature of interactions being considered beyond that of feeding interactions. The third assesses different sources of social impact and the species at risk of extinction, and topological repercussions of their loss. The fourth examines the inclusion of humans, their activities and their interactions within food webs. Each of these topics is addressed in this chapter, although my focus on socio-natural interactions means that the emphasis lies on the last two. This chapter has the following aims:

- to identify those species most at risk from the different sources of social impact identified in Chapter 2;
- to assess the likely repercussions on food web topology of their loss; and,
- to examine how ecological and social networks could be combined.

The chapter is structured as follows. The ecological nature of highly-connected species, whether of feeding or other networks, is discussed in Section 6.2. This section briefly summarises recent discussions arguing for re-definition of the terms 'keystone species' and 'ecosystem engineer'. These are but two terms used to indicate that some species in ecological communities are more crucial to its structure and function than others.

Section 6.3 addresses the first aim above. It returns to the four sources of social impact discussed in Chapter 2 and attempts to identify the features of species that would make them more vulnerable to extinction. On the basis of this discussion, Section 6.4 devises alternative species removal sequences, reflecting social impact, and tests them on the two food webs used in Chapter 5. This corresponds to the second aim above. Section 6.5 addresses the third aim. Predation matrices, from ecology, and input-output (I-O) tables, from economics, document interactions between pairs of system components. The two techniques are compared and their extension to include the other system assessed.

Section 6.6 summarises the discussion and presents my analytical framework for assessing the repercussions for coevolution of alternative environmental management regimes. This framework is applied in Chapter 7, and discussed again and evaluated in Chapter 8.

6.2 Are keystone species and ecosystem engineers highly-connected?

The notion of the keystone species derives from both ecology and conservation biology. It emphasises that species are not equal in contributing to community structure and function. Abundant and dominant species are important because they give support to a community. Odum (1971) uses the term key species. Other species may also be important because, despite their relatively low abundance, they sustain the community by keeping its diversity high (Barbault *et al*. 1991; Bond 1993; Mills *et al*. 1993). These are keystone species (Piraino *et al*. 2002).

The term draws from the stone at the top of an arch that keeps the arch from falling (see Figure 6.2). Initially its definition derived from predator control (Paine 1969). A keystone predator controls potentially dominant prey species that would otherwise monopolise a community and keep its diversity low. The keystone-species quickly became a paradigm in community ecology (Mills *et al*. 1993), but became too widely extended and, as a result, has been criticised for ambiguity (Strong 1992; Mills *et al*. 1993). It was redefined: a keystone species has an impact on its community that is large, and disproportionately large relative to its abundance (Power *et al*. 1996; Simberloff 1998). This definition explicitly excludes structural and other dominant species.

The keystone attribute has been unsuitably applied to ecological dominants (Piraino *et al*. 2002; various references cited), some of which are better considered key species due to their bio-architectural complexity. Examples include plants, corals and other less-known reef-building invertebrates. Application of the keystone label to species other than predators has led also to proliferation of sub-terms (see electronic appendix 1 of Piraino *et al*. 2002), each referring to a specific mode of action or behaviour.

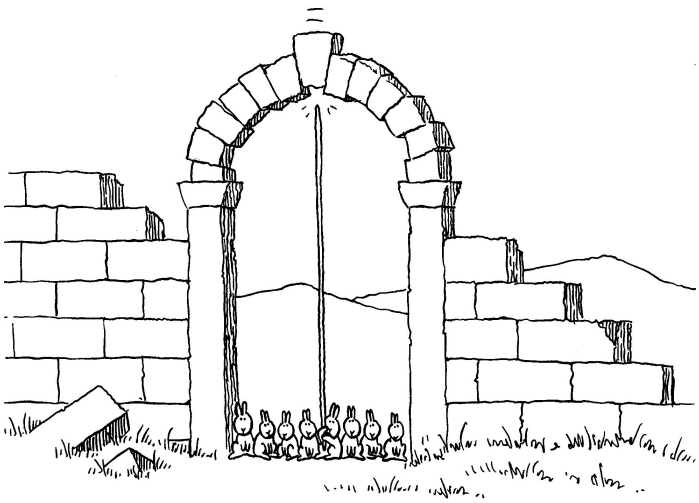


Figure 6.2 The keystone prevents the stones in an arch from collapsing (from "Return of the Bunny Suicides" by Riley 2005)

The keystone effect has also been recognised in contexts other than feeding interactions. All organisms modify their environments. Such niche construction can have profound effects on the distribution and abundance of organisms, with species depending on others for their habitat (Laland *et al*. 1999). Examples include birds nesting in the holes in trees, anemones attaching to the shells of hermit crabs, and the fauna supported by bromeliads in the water trapped at the base of their dense leaf-rosettes. Niche construction establishes engineering networks (Jones *et al*. 1994). Such networks do not conform to the same principles of mass flow, conservation of energy etc. that govern food webs, and so are likely to be more difficult to analyse. Jones *et al*. also proposed the term 'ecosystem engineer' – an organism that directly or indirectly modulates the availability of resources to other species by causing physical state changes in biotic or abiotic materials. Ecosystem engineers may also display keystone functions (Piraino *et al*. 2002), but the engineering property is distinguished from the keystone property. An ecosystem engineer is an organism that directly or indirectly modulates the availability of resources to other species by causing physical state changes in biotic or abiotic materials.

Solé and Montoya (2001) and Jain and Krishna (2002) have suggested that highly-connected species in food webs might be keystone species, or at least perform a keystone function. It can be similarly argued that an ecosystem engineer is a hub in engineering networks. Both sets of authors argued that the definition of a keystone species should be enlarged to accommodate the potential for secondary extinction and network fragmentation as a consequence of their loss. The notion is appealing. Highly-connected species can be expected to be intermediate consumers, having links to both predators and prey. As such, they may function in top-down control on prey species, as well as bottom-up, resource limitation on predators. The water flea, *Daphnia*, provides an example, controlling phytoplankton at the same time as serving as food for fish. However our current knowledge is insufficient to make generalisations on this score, and the picture may not be quite so simple.

Jordán and Scheuring (2002) argued that positional importance in a network, rather than connectedness, is a better indicator of keystone function. Positional importance takes

into account indirect or higher order interactions among species. A species on which a hub depends might also be viewed as a keystone species, as illustrate in Figure 6.3. In the left hand network, species 15 is highly-connected while species 5 is poorly-connected. Removal of either species has the same effect on the network, shown in the right hand network.

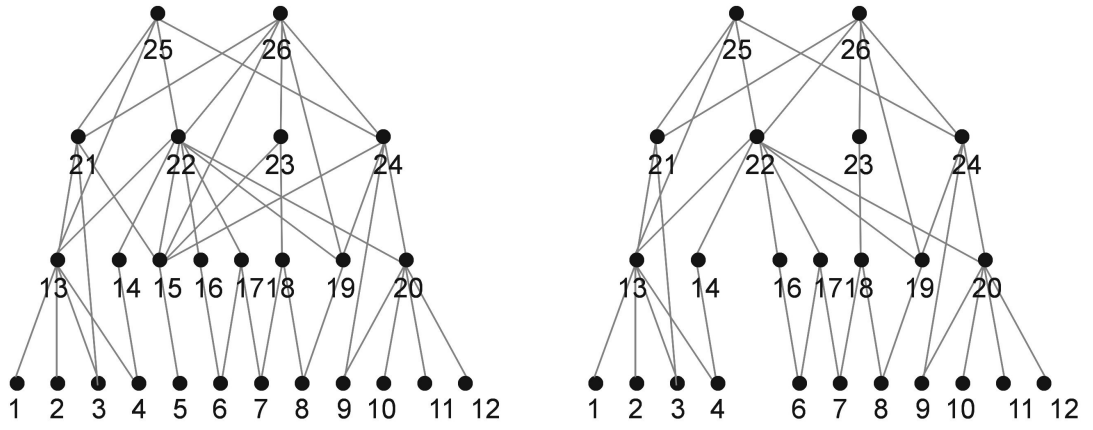


Figure 6.3 The removal of highly-connected species 15 has the same effect on the network as the removal of poorly-connected species 5

Highly-connected species in food webs direct matter and energy towards themselves, then channel them to higher trophic levels. This could mean that their populations have a high biomass. If so they are more likely to be dominant or key, rather than keystone, species. The equation of keystone with high-connectedness is not only uncertain, but it might also reduce the clarity of a concept which, as discussed above, has already been variously defined and applied. It is not yet possible to answer the question that is the title for this section. However a network perspective could make an important contribution to our thinking about which species play crucial roles in community stability maintaining community structure and function.

6.3 Social antagonism and ecological networks

6.3.1 Introduction

The node removal protocols used by Dunne *et al*. (2002b) bear little relationship with real-world species loss. There is no *a priori* reason why species loss should be random, should target highly- or poorly-connected species, or should exclude basal species. This section combines the sources of social impact identified in Chapter 2, with current knowledge of complex networks as presented in Chapter 4, to develop a network perspective on social antagonism. Feeding interactions are seen as the main interaction within ecological communities, and so food webs have received the bulk of attention as ecological networks. Engineering networks based on habitat interactions have also been proposed, but have not yet been the focus of much analysis. Humans are quite clearly a major force within many ecological networks, not just feeding networks. The following discussion translates social antagonism into changes in network topology, by identifying species at risk of extinction and making assumptions about the nature of such species in

networks. Where possible, the effects on food webs and engineering networks are distinguished, but it is to be expected that these two ecological networks overlap each other as well as other ecological networks. Table 6.1 summarises the species most at risk from social impact, and likely effects on networks of their loss. This table forms the basis of the removal sequences simulated in Section 6.4.

Table 6. 1 Expected effects on ecological networks of species extinction from different sources of social predation

Source of social impact	Network features of species most at risk	Possible effects on food webs	Possible effects on engineering networks
Social predation	Highly connected (hubs) Large-bodied and/or abundant Mainly vertebrates, occasionally plants and invertebrates	Decreased robustness Decreased stability with predominance of strong interactions and spatial displacement of detritus feedbacks	Effects greatest should a hub in food webs also be a hub in an engineering web
Emissions			
a) direct effects	Poorly-connected	Decreased robustness only with large-scale loss of species	Decreased robustness only with large-scale loss of species
b) bioaccumulation	Higher-order predators, some of which may be highly-connected	Reduced robustness Reduced top-down controls on prey	Uncertain
c) nutrients	Basal species	Change to primary energy source → restructuring, esp. of lower trophic levels	Change to primary habitat → restructuring of network and possible regime shift
d) Greenhouse gases	Species with small geographical ranges	Impacts subsequent to disruption of engineering networks	Fragmentation with secondary losses
Habitat loss and fragmentation	Basal species and ecosystem engineers Endemic species Large-bodied vertebrate consumers	Vertical compaction and blunting of food webs	Fragmentation with secondary losses following loss of basal species
Biotic exchange	Competitors and their predators Prey of invasive species	Emergence of new hub, with fragmentation and secondary extinction	Fragmentation with secondary losses, esp. if invader is a basal species

6.3.2 Social predation and ecological networks

Humans are part of many food webs via social predation. We are omnivores, exploiting multiple trophic levels. We harvest various plants and hunt various consumers. We are also top predators since we have developed effective defence against potential predators

and many parasites. Our use of species is not restricted to their ingestion. Their biomass may be used for fuel, as raw materials or as ornaments. We may also prey on species because they threaten us, either as predators or as competitors for the resources on which our lifestyle depends. We have been particularly effective as consumers in food webs, excluding competitors and redirecting matter and energy flows to service our own needs.

Humans have historically been part of many food webs. As early human populations increased and human societies moved away from hunter-gather to modern lifestyles, our participation in food webs has also changed. These changes fall into three broad categories: reduced omnivory, increased interaction strength, and spatial displacement of detritus feedbacks. Each of these changes can have implications for the robustness of food webs and the stability of ecological communities.

Humans have become less dependent on naturally-occurring species as a source of food. Domestication has brought species within the social system. Our predominant links with food webs now revolve around forestry and fisheries, although forestry, particularly clear felling, falls more under habitat loss and fragmentation. The poaching of protected and/or endangered species such as elephants, rhinoceroses and gorillas, and extraction beyond a population's ability to regenerate pose the greatest extinction risks to species. A growing human population means a growing demand for protein and raw materials. Combined with technological advancement, we are now able to exploit resource stocks efficiently, to harvest stocks far-removed from where we consume them, and to target new species in previously untouched food chains.

Assumption 1: social predation targets highly-connected species and species with a large body size

As was discussed in Chapter 2, prey of social systems has a high value per unit mass. Value is a balance between consumer preferences and extraction costs. Costs tend to be low when the target species is large, abundant, and/or easily accessed. Vertebrates have generally achieved the largest body sizes and so have received the largest attention from humans as prey, although there are exceptions, such as mussels, prawns and lobsters from in aquatic ecosystems. Our prey also tends to be intermediate consumers, such as turtles, various ungulates and other large herbivores. Top predators are taken more because they are competitors or because of their ornamental value. Fisheries tend to target higher-order consumers, although recent trends show that we are exploiting more species from lower trophic levels – 'fishing down the food web' – due to overfishing and the use of fishmeal in aquaculture and intensive agriculture (Pauly *et al.* 1998).

Large size and abundance indicates that a species is successful in acquiring resources and converting them into biomass. Such a species can be assumed to play a leading role in directing matter and energy through food webs. Chapter 2 cites authors who argue that such species, particularly in aquatic food webs, are keystone species. I would argue that it is more likely that such species are highly-connected and that social predation is therefore targeting hubs. If social predation places species at risk of extinction, it is also increasing the risk of fragmentation and secondary losses from the food web. This risk will only increase when more than one species in a food web is being targeted.

Our vastly improved efficiency in resource extraction and exclusion of competitors means that interactions between humans and extracted species are strong. Ecologists measure interaction strength as the slope (derivative) of the function relating the density of species A to the density of species B. If the slope is very steep, and an increase in A causes a large decrease in species B, then the interaction strength is large. As shown in Chapter 2, the stability in ecosystems appears to be related to patterns of interaction strengths, with strong interactions coupled to weak interactions that mute their destabilising potential. By excluding competitors and extracting targeted species efficiently, social predation is simplifying food webs, replacing networks of mixed interaction strengths with chains of strong interactions. This will compromise network robustness and ecosystem stability.

Globalisation caters for the spatial displacement between extraction and consumption. Flows of dead matter to a detritus component at the bottom of food webs give large, positive, top-down effects. Such flows become stronger in more developed, complex ecosystems, and enhance their stability (see Chapter 2). Social predation means, not only that the production of many food chains is being siphoned off to social systems at a distance, but also that the large, top-down effects of detritus feedbacks are displaced. They have become concentrated in some places, notably large urban centres, and diluted in others, such as the ecosystem where prey species are found. This is also a source of destabilisation of ecological communities.

6.3.3 Emissions and ecological networks

To consider the effect of emissions on ecological networks, substances are grouped into four categories:

1. substances that directly affect the fitness components of species (survival, reproduction, etc), such as pesticides and endocrine disruptors;
2. substances that tend to bioaccumulate, such as heavy metals, organochlorines and their metabolites;
3. substances needed by organisms, but not usually found at high levels, such as macro- and micronutrients; and,
4. substances that effect large-scale change to habitats, such as greenhouse gases.

Assumption 2: toxicity affects poorly-connected species

The first category of emissions tends to affect sensitive species. Ecologically sensitive species would seem more likely to be poorly- than highly-connected. If so, only the loss of a number of such species would have an adverse effect on network robustness. Much depends on the nature of the substances and the route by which they affect species.

Assumption 3: bioaccumulation affects top predators

The second category comprises substances that accumulate in organisms and magnify up food chains. The largest concentrations and greatest effects are on top predators, as typified by the effect of DDT on eggshells of the peregrine falcon. Top predators are unlikely to be hubs. Highly-connected species are often intermediate consumers with links to higher and lower trophic levels. Bioaccumulation that adversely affects the higher intermediate consumers, some of which could be hubs, would adversely affect

food web robustness. The loss of one or more top predators will change top-down controls on intermediate consumers and is more likely to affect network robustness through the mix of strong and weak interactions.

Assumption 4: nutrient enrichment affects basal species

The third category can comprise a large number of substances, but is best exemplified by nutrients that limit plant growth. Vegetational complexes tend to be dominated by species that are highly competitive in obtaining limiting resources. Increases in nutrient concentrations change competitive balances, benefiting some to the detriment of others. It leads to shifts in plant species composition, as discussed in Box 2.3. Both food webs and engineering networks will be affected.

Plants are basal species in food webs. Changes in plant species composition are likely to percolate throug food webs via both herbivore and detritivore chains as a result of the different kinds of plant material available for consumption. The physical structure of many ecosystems is determined by dominant plant species that give shape and form as a result of standing rooted in sediments and growing upwards towards light. Changes in plant species composition can change structure and so habitat. Many of the original occupiers of an ecosystem's ecospace may no longer be supported. For example, changes to both food webs and engineering networks can be inferred in freshwater lakes under nutrient loading, as algae replace macrophytes. Fragmentation and secondary species loss in such conditions are indicated by declining species richness (Jørgensen & Richardson 1996; Nixon 1995) and regime shifts (Scheffer & Beets 1994; Hosper 1997; Scheffer *et al*. 2001; Scheffer & Carpenter 2003).

Assumption 5: climate change affects species with small geographical ranges

Finally, greenhouse gases are believed to cause climate changes. Climate – temperature, volumes and nature of precipitation, seasonal patterns – is a prime determinant of habitat, and its change can be expected to have impacts on many species. Climate change is suspected to be the cause of a number of past extinction events (see Chapter 2). Two aspects with network implications are highlighted from the literature on extinction. The first is the inverse relationship between extinction rate and geographical range as indicated by the fossil record (references cited by Rosenzweig 2001). Modern studies over shorter time scales also display an inverse correlation between extinction rate and area (Rosenzweig 1995 – see also Chapter 2), suggesting that species with small geographical ranges will be the most adversely affected. A large geographic range could indicate exploitation of multiple networks.

The second aspect is that survivorship and extinction during mass extinction events often fails to coincide with patterns during 'normal' times with background extinctions (see Chapter 2). Mass extinction events can remove the successful incumbents of ecosystems, not just the marginal players that normally would be at risk of extinction. An explanation for the loss of such species is that the robustness of their ecological networks was compromised. Network fragmentation could have lead to the secondary extinction of previously successful species.

6.3.4 Habitat loss and ecological networks

Chapter 2 summarised the species-area relationship (SAR), which describes the increase in species richness as the area of an ecosystem increases. Current findings with regards to the converse, loss of species with loss of area, was also discussed. Studies to date suggest that species loss with habitat loss is linear. But which species are lost?

Much research elucidating the effects of species loss on ecosystem functioning (see Tilman *et al*. 2002 and Petchey and Gaston 2002 for reviews) creates experimental diversity gradients by assuming random community assembly or disassembly. However natural and anthropogenic diversity gradients clearly show non-random patterns in the order and characteristics of species lost (various references cited by Duffy 2003). Since plants are the primary species lost when humans convert habitat to their own purposes, experimental studies have tended to focus on loss of plants when examining ecosystem function. The respective roles of competition, facilitation and sampling are examined but little is said about trophic interactions and the role of consumers, despite extensive documentation of the impacts of consumers on ecological structure and function in a wide range of ecosystems (Schmid *et al*. 2002; Díaz *et al*. 2003; Duffy 2003).

Extinction risk in both plants and animals is exacerbated by rarity, small population size, small geographical range, slow population growth, and specialised ecological habits (e.g. Pimm *et al*. 1988; Lawton 1995; Didham *et al*. 1998; Purvis *et al*. 2000). While habitat loss poses a significant threat to plants, the threat is non-selective in that extinction is a consequence of reducing the habitat as a whole. Duffy 2003 argues that, all else being equal, habitat loss should then be most detrimental to endemic species at low population densities. He argues that these factors make large vertebrate consumers that interact strongly with other members of the ecological community, vulnerable to extinction. For example, loss of a few predator species often has impacts comparable in magnitude to those stemming from a large reduction in plant diversity..

Assumption 6: habitat loss affects large vertebrates and top predators

The above demographical risk factors are characteristic of animals in the higher trophic levels of food webs. Top predators in particular should be especially vulnerable to habitat destruction (Pimm *et al*. 1988; Lawton 1995). Both model systems and field observations confirm that top predators are differentially lost under habitat alteration (Didham *et al*. 1998; Gilbert *et al*. 1998; Petchey *et al*. 1999). The most vulnerable species are large vertebrate consumers (Duffy 2003). Vulnerability is aggravated by the lower species richness of large vertebrates, which results in less redundancy and less potential for functional compensation. Consequently the most predictable effect of habitat loss is a skew in trophic structure caused by a vertical compaction and blunting of the trophic pyramid as a result of proportionally greater losses of species from the higher trophic levels.

6.3.5 Biotic exchange and invasive species

Biotic exchange is the human-mediated addition of species to ecological networks. Concerns lie with the homogenisation of biotas and adverse impacts on economic and ecological systems. Introduced and invasive species can adversely affect the abundance of endemic species in a number of ways including: predation, competitive suppression,

changes in disease incidence, and changes in the physical habitat such as fire frequency or nutrient cycling (Tilman and Lehman 2001). Invasion is often paired with local extinction. Should some of these lost species be hubs, or should an introduced species emerge as a hub, the way is paved for secondary extinction and network fragmentation.

Assumption 7: an invasive species is a newly-emerging hub or top predator

The move from introduced to invasive is poorly understood. One factor in this ecological shift could be that growing abundance and effectiveness channelling of resources into its own biomass coincides with emergence as a new hub in ecological networks. This could lead to reduced robustness, fragmentation and secondary extinction. It is very difficult to make generalisations, but invasive species often display at least one of two features that can be interpreted in terms of network topology: they exclude at least some competitors, and they are not subject to predation in their new environment.

A highly competitive invader changes balances among those competing for the same resources. When the invader is also a consumer, the interaction strength on prey species increases. This will be exacerbated by exclusion of competitors, and the balance between weak and strong interactions may be disrupted. Some prey species may become extinct. Many invasive species have been introduced into new environments without their natural predators, and so are not subject to top-down controls on population size. The predators of excluded competitors may also face extinction. The net result of these factors is the funnelling and accumulation of energy in a single direction – towards the invasive species. The food web is less rich in species and probably dominated by large interaction strengths. Available knowledge suggests that such a food web would not be robust.

Invasive plant species have broader effects on ecological communities and networks. Firstly, competitive exclusion of other basal species means that some herbivores will be lost and food webs will be restructured. Secondly, an invasive plant can dominate a particular habitat. This can be expected to lead to major restructuring of engineering networks.

6.4 Species removals to capture social impact

6.4.1 Introduction

Section 6.3 identified features of species most at risk from social impact. This section identifies species from the El Verde rainforest and St. Marks seagrass food webs with these features, and then examines changes to food web topology with their removal. The exercise parallels that undertaken in Chapter 5 but with more realistic species removal that captures the effects of social impact according to the assumptions developed the previous section. The purpose is to understand how social impact could be affecting food web topology, and whether topological network analysis might be useful in predicting the likelihood of major changes in future ecosystem states. The focus is on the left hand side of Figure 6.1, and changes within the natural system as a result of social impact.

6.4.2 Social predation

Fishing and hunting are used to illustrate social predation. Both target large-bodied and/or abundant species that could be highly-connected (see Assumption 1 above). Species tend to be vertebrates consumers such as fish, turtles, birds and mammals. Consumers derive from all trophic levels of both detritivore and grazing food chains. Small herbivores such as zooplankton and insects, and some top predators such as sharks and snakes, are less likely to be targeted.

A selection from the 25% most highly-connected species in the rainforest and seagrass food webs was made. Species IDs and criteria are given in Table 6.2 (see Chapter 5 Appendices III and IV for species names). The change in connectance with removal of these species and the number of primary and secondary losses are given in Table 6.3.

Table 6. 2 Highly-connected species at risk of extinction due to social predation

	El Verde rainforest	St. Marks seagrass
Criterion for removal:		
- large intermediate consumers, vertebrates	12, 13, 14, 15, 16, 17[1] 19, 20, 21 23, 24, 25[1]	19
- small but presumably abundant intermediate consumers, vertebrates	30, 31, 32, 33,3 8[1]	1
- large invertebrates	34, 35	9
- presumably abundant invertebrates in detritivore chains	135	15, 35
- top predators		5

1 closely related species

Table 6. 3 Effects of removal of species vulnerable to social predation

	El Verde rainforest		St. Marks seagrass	
	No.	%	No.	%
Primary species removals	20	12.8	6	12.5
ΔC_{stand}	-0.023	-41	-0.011	14
Secondary species losses	7	4.5	1	2.1

This removal sequence is similar, but not as extreme, as the sequence removing the most connected species in Chapter 5. It causes large negative changes to connectance and secondary loss of species. The rainforest is more heavily affected than the seagrass.

6.4.3 Emissions

Table 6.1 identified sensitive, possibly poorly-connected species, top predators and other high order consumers, basal species, and species with small geographic ranges as being most vulnerable to emissions (see Assumptions 2-5 above). I test the effects on network topology of bioaccumulation and nutrient enrichment (Assumptions 3 and 4), and so remove high order consumers and basal species from the two food webs. High order consumers are lost because bioaccumulation affects their fitness. The loss of basal species occurs as a consequence of altered competitive balances with nutrient enrichment.

Bioaccumulation

I have assumed that trophic level and the number of links to lower species in the food web determine vulnerability to bioaccumulation. The former derives from the literature; the latter provides maximum exposure to contaminants. Top predators and higher order consumers were identified from both webs, and the number of species one and two links below was counted (i.e. prey, and the prey of prey). Table 6.4 shows results for all top predators and some of the more highly-connected higher order consumers.

Table 6. 4 Number of species one and two links away from top predators and select secondary consumers (highlighted species were identified as being most vulnerable to bioaccumulation)

Trophic level	Species ID	No. species 1 link away	No. species 2 links away
El Verde rainforest:			
top predators	**1**	**22**	**356**
	2*	**20**	**434**
	3*	**20**	**372**
	4	5	114
	5	**22**	**336**
	6*	**19**	**380**
	7*	**24**	**468**
	8*	8	255
	9	17	133
high order consumers	10	27	351
	12	**62**	**677**
	13	38	257
	14	39	294
	21	35	446
	23	47	357
	25	43	369
St. Marks seagrass:			
top predator	**41**	**3**	**18**
high order consumers	28	7	34
	38	9	16
	39	**9**	**100**
	40	**7**	**93**

* Also consume species 12, identified as the most vulnerable secondary consumer

Species highlighted in Table 6.4 were removed from the food webs and the results are summarised in Table 6.5. As can be expected, loss of top predators did not lead to secondary extinctions. The loss of species 12 from the rainforest always results in the loss of species 113, which is parasitic only on species 12. The main effect of removing top predators was the creation of new top predators - consumers initially in a lower trophic level that are no longer subject to predation. With the loss of the highest trophic level, the food web becomes compacted. This removal sequence caused connectance to decline for both webs indicating reduced robustness. The decline was slightly greater for the rainforest than the seagrass web despite proportionately fewer removals.

Table 6. 5 Effects of removal of species vulnerable to bioaccumulation

	El Verde rainforest		St. Marks seagrass	
	No.	%	No.	%
Primary species removals	7	4.5	3	6.3
ΔC_{stand}	-0.004	-6.4	-0.004	-4.6
Secondary losses	1	0.6	0	0

Nutrient enrichment

Basal species were removed from the two webs to test the effects of nutrient enrichment. This experiment is more artificial than the rest. Removal of the trees or of the seagrass means loss of the ecosystem's key species. Nutrient enrichment usually means the replacement of one basal species by another. The time over which basal species are lost is not specified. Nutrient disturbances are dynamic. It is the rate of removal that matters, and whether that rate can be compensated by continual growth.

In both food webs, removals were carried out in three steps. The first removed live plant tissue from both webs. For the rainforest, this means plants, live leaves, live wood, sap, roots, pollen, nectar, fruits, seeds and flowers; for the seagrass, this means *Halodule wrightii* and its epiphytes. The second removed dead plant tissue from the rainforest web – dead wood, leaves and roots for the rainforest. The third removed detritus from the rainforest web, and detritus and benthic bacteria from the seagrass. The effects on the two webs are shown in Table 6.6.

Table 6. 6 Effects of the removal of basal species as a result of nutrient enrichment

	El Verde rainforest		St. Marks seagrass	
	No.	%	No.	%
Live plant material				
- primary species removals	10	6.4	4	8.3
- ΔC_{stand}	+0.012	+18.4	+0.006	+8.1
- secondary losses	22	0.14	0	0
Dead plant material				
- primary species removals	14	9.0		
- ΔC_{stand}	+0.016	+26.2		
- secondary losses	2	1.3		
Detritus, benthic bacteria				
- primary species removals	1	0.6	6	12.5
- ΔC_{stand}	+0.028	+44.6	+0.008	+11.2
- secondary losses	14	9.0	2	4.2
TOTAL primary removals	26	16.0	10	20.9
TOTAL secondary losses	37	23.8	2	4.2

Loss of basal species caused extensive secondary extinctions in the rainforest web, which lost 22 species in a cascade when live plant material was removed, and a further 14 species, also in a cascade, when detritus was removed. The number of secondary losses exceeds primary removals. The seagrass web lost only 2 species secondarily. The

increase in connectance for both webs indicates that both primary and secondary losses were poorly-connected species. The milder effect on the seagrass again suggests again that it is the more robust.

The rainforest web did not fragment despite substantial secondary losses. The remainder of the rainforest web comprises some 100 species, only one of which is capable of photosynthesis (lichens). Such a situation is impossible, at least without substantial energy imports. Close examination of the rainforest food web shows that many highly-connected secondary consumers are involved in mutual interactions – species *a* eats species *b* while species *b* eats species *a* – and in short trophic loops. A trophic loop is a pathway of interactions from a given species through the food web back to the same species without visiting other species more than once (see Chapter 2). A number of trophic loops involving species 12 are illustrated in Figure 6.4. Species 12 is the most-connected species in this web. It eats 64 species, and is in turn eaten by 15 of them. It is also cannibalistic. The grey, stippled lines in Figure 6.4 indicate return flows completing a trophic loop; in two cases these return flows also indicate mutual interactions.

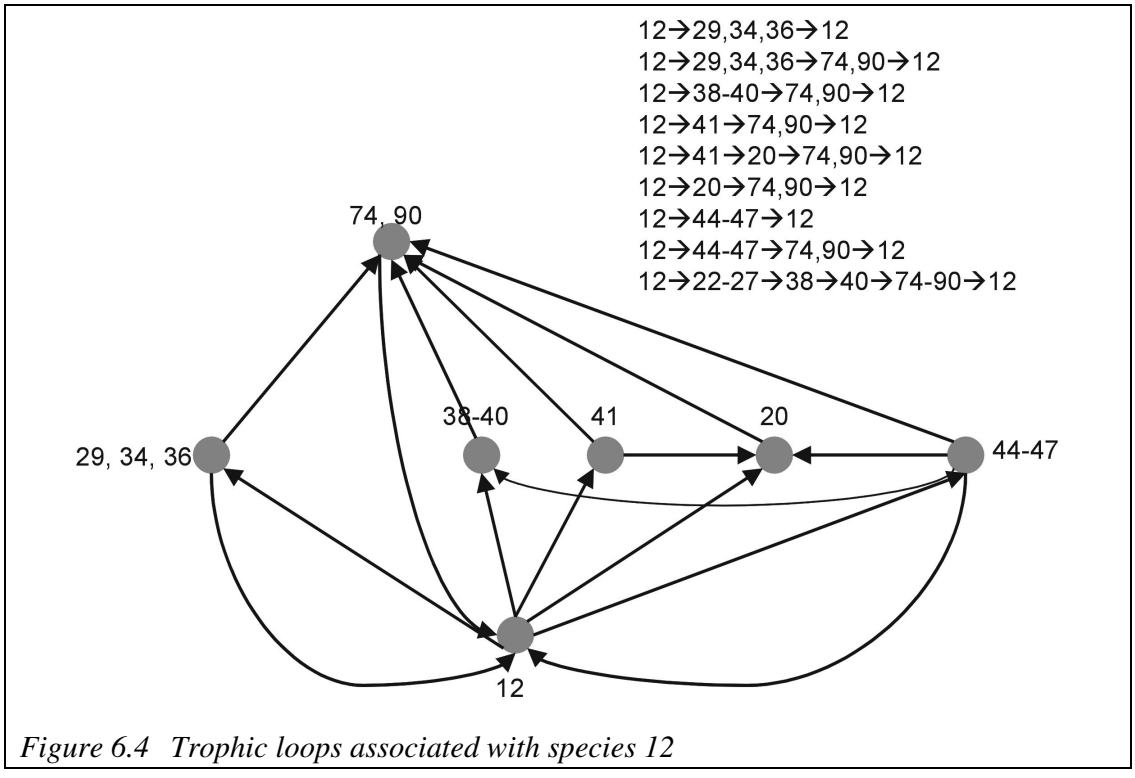


Figure 6.4 Trophic loops associated with species 12

Other species figure in short trophic loops. A quick scan of the predation matrix is enough to see that highly connected reptiles, amphibians and arthropods engage in mutual interactions. Species 74 and 90 engage in mutual interactions, as well as being the main reason for short trophic loops (see Figure 6.4). These two 'species' are an amalgamation of a large number of taxonomically similar species. Species 74 consists of 158 species of flies, and species 90 of an unspecified number of nematodes. In the case of the flies, mutual interactions can easily be envisaged when the fly is prey, say for amphibians and reptiles, as well as parasitic on these species.

A food web cannot maintain itself on mutual interactions and short trophic loops among consumers. Every interaction involves energy losses, and without a source of energy, the

system will 'wind down'. This is not indicated in the above topological network analysis. The amount of energy transferred per interaction, not merely its presence or absence, is needed to provide insights as to the future of a food web with loss of basal species. A purely topological network analysis is insufficient to address the issue of nutrient enrichment.

6.4.4 Habitat loss and fragmentation

Section 6.3 identified basal species, endemic species at low population levels, and large-bodied vertebrates as the most vulnerable to habitat loss and fragmentation. Loss of basal species was examined in Section 6.4.3. It might be possible to identify endemic species from the rainforest and seagrass food webs, but I have is no information on their population sizes. Consequently, this section focuses on the loss of large-bodied vertebrates and Assumption 7 above.

Table 6.7 categorises vertebrates from the two webs according to size, taxonomy and trophic level. Categories have been ranked for vulnerability. A rank of 1, the most vulnerable to extinction from habitat loss, has been assigned to large-bodied, vertebrate top predators. The lowest rank corresponds to lower order and smaller vertebrates. These categories of species were then removed from the two food webs in order of their vulnerability to habitat loss, beginning with the most vulnerable. Table 6.7 summarises the effects on the webs, and Figure 6.5 shows the changes in connectance plotted against total species loss.

Table 6. 7 Effects of removing categories of species vulnerable to habitat loss

Rank	Category	Primary species losses		ΔC_{stand}		Secondary species losses	
		No.	%.	Δ	%	No.	%
St. Marks seagrass:							
1	top predators	1	0.001	1.7	2.1		
2	intermediate consumers - birds	5	0.011	14.2	12.5		
3	intermediate consumers - fish	3	0.015	22.6	18.8		
4	intermediate consumers - fish	9	0.041	66.2	37.5		
El Verde rainforest:							
1	top predators	9	0.007	12.1	5.8		
2	higher consumers – mammals	1	0.008	14.2	6.4		
3	higher consumers – reptiles	5	0.017	30.0	9.6		
4	higher consumers – birds	7	0.025	45.1	15.4	2	1.3
5	higher consumers – amphibians	7	0.039	68.6	21.2	3	1.9
6	intermediate consumers – mammals	1	0.039	69.1	22.4	1	0.6
7	intermediate consumers – reptiles	4	0.042	75.0	25.0		
8	intermediate consumers – birds	11	0.049	86.1	32.1		
9	intermediate consumers – amphibians	1	0.049	87.1	33.3	1	0.6

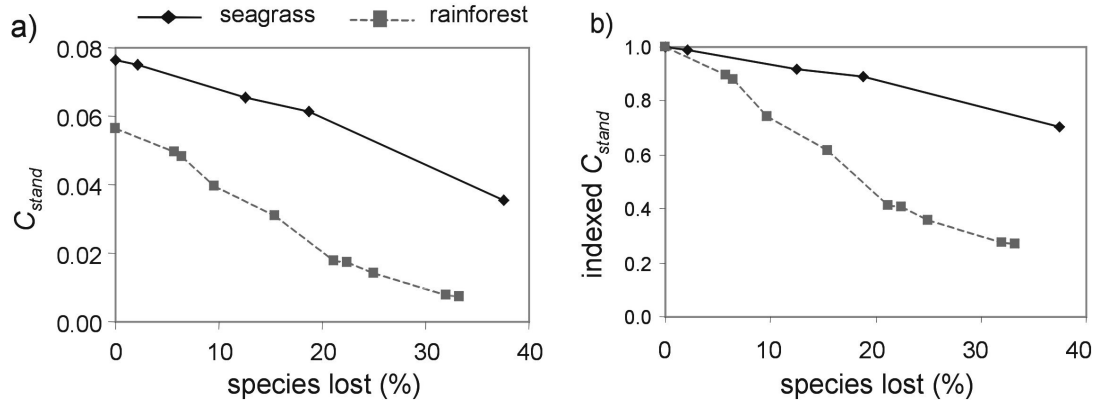


Figure 6.5 Effect on connectance and indexed connectance of removing species vulnerable to habitat loss; loss protocol was determined by rank in Table 6.7

Approximately one-third of species were removed from the two food webs; half of these species were ranked in the top 25% of highly-connected species. The impact of removing such well-connected species is clearly seen in the sharp decline in connectance. Impact is more severe on the rainforest, which also lost species secondarily. The rainforest food web is clearly much more vulnerable to habitat loss than the seagrass food web. The impact on its connectance is almost as severe as the loss of the most-connected species in Chapter 5.

The corresponding area of habitat lost has not been specified. As discussed in Chapter 2, studies to date suggest a linear relationship between loss of species and loss of habitat. Assuming a linear and continuous relationship, three forms can be distinguished based on assumptions as to when there are no species, or no habitat left. The simplest is that the line passes through the origin, so that *x*% habitat loss means *x*% loss of species. This means that zero species occurs with zero habitat. The second argues that there is a critical area requirement for some ecological communities, so that the last remaining species succumb when habitat declines below some threshold. This can be expected to be the case when species in a community are largely endemic. The rainforest food web probably has a high proportion of endemic species. Communities with a high proportion of transient species or species with large geographical ranges could be expected to display the third form, where some proportion of species remain even with complete habitat loss. Such species would be able to switch their resource needs to other food webs. The seagrass food web comprises many such species due to its 'nursery function'. Consideration of the possible form of the relationship between habitat and species loss also suggests that the rainforest would be more vulnerable to habitat loss.

6.4.5 Biotic exchange

The topological effects of invasion by a single species have been simulated on the rainforest and seagrass food webs. An invasive species may come to occupy any trophic level. Invasive top predators, intermediate consumers and basal species have been simulated. The invader is assumed to exclude competitors and to take over all of their links to prey. Further it is assumed that the invaders are not subject to predation by higher order consumers. The results of these changes to the webs are summarised in Table 6.8.

Table 6.8 Possible effects on food web topology with biotic exchange

	El Verde rainforest			St. Marks seagrass		
	ID	No.	%	ID	No.	%
Top predators	1-9					
primary removals		9	5.8			
ΔC_{stand}		-0.004	-6.4			
secondary losses		0	0.0			
Intermediate (1) *	12-17			25-27		
primary removals		6	3.8		3	1.9
ΔC_{stand}		-0.014	-24.2		-0.005	-6.2
secondary losses		1	0.6		0	0.0
Intermediate (2) *	22-25					
primary removals		4	2.6			
ΔC_{stand}		-0.007	-11.7			
secondary losses		0	0.0			
Intermediate (3) *	74			12-15		
primary removals		1	0.6		4	2.6
ΔC_{stand}		-0.001	-2.1		-0.014	-17.9
secondary losses		0	0.0		0	0.0
Primary plants	140-149			43-45		
primary removals		10	6.4		3	1.9
ΔC_{stand}		-0.017	-29.2		-0.004	-5.3
secondary losses		22	14.1		0	0.0

* Intermediate (1) and (2) are higher order consumers and vertebrates; intermediate (3) are lower order consumers and invertebrates.

An invasive top predator in the rainforest food web replaces the existing nine top predators, feeding on all of their prey. It is likely that the replacement of many by one top predator will change interaction strengths, and could drive some prey species to extinction. However changes in interaction strength cannot been simulated. Invasion effects a negative change in connectance and to cause no secondary extinctions. Since there is only one top predator in the seagrass web (raptors), this form of invasion makes no topological change to the web.

A large number of possibilities for invasion at intermediate levels can be envisaged. I have formulated a selection of 'worst case scenarios' based on two assumptions. Firstly, the invader is assumed to exclude competitively a functional group of species feeding on similar prey. In the case of the rainforest, these species are also closely related taxonomically. Secondly, the functional group includes one or more highly-connected species. As shown in Table 6.8, invasion causes negative changes to connectance in both food webs and, in one case, triggered secondary extinction.

Only changes to live plant tissue are considered with an invasive basal species. Invasive basal species differ from other invasions because they do not prey on other species and, in turn, are not subject to herbivory. The invader does not become part of the food web even though it is clearly part of the community. Invasive plants, by out-competing other basal species for resources, effect topological changes similar to those discussed under nutrient enrichment.

It is difficult to generalise the results. However, I highlight the following.

The loss of top predators from the rainforest causes a mild negative change in connectance. None of the original top predators is among the most highly-connected species, but the invader, who takes over all top predator links to prey, becomes the third most highly-connected species. It has clearly emerged as a new hub.

Intermediate (1) causes the greatest change to connectance of the rainforest web. Five of the species lost are among the top-ten connected species. The number of links to prey was generally more than the number of links to predators, and these species were involved in many mutual interactions. In subsuming all of competitors' links to prey without passing biomass on to predators, many links are lost from the network. This causes the relatively large negative change to connectance. Even though the invader is not consumed, it becomes one of the most-connected species, emerging as a new hub and a new top predator.

The greatest change to the seagrass web's connectance is effected by loss of lower order consumers, as shown in Intermediate (3). As with Intermediate (1) in the rainforest, most of the removed species are very highly-connected and engaged in mutual interactions. However the connectedness of these species comes primarily from their links to higher order consumers, rather than links to their prey. Since the invader is not consumed, it becomes a poorly-connected top predator and probably does not emerge as a new hub.

The issue of resolution is highlighted with the loss of species 74 from the rainforest (Intermediate 3). Resolution reflects the degree to which components of a food web are taxonomically distinguished (Martinez 1991). 'Species 74' consists of 158 species of flies. While this is common with smaller species (most of the invertebrates in the rainforest are not taxonomically distinguished to the species level), it creates inconsistencies when larger species are so distinguished. To illustrate, intermediate (1) for the rainforest removes six species of the same genus, all of which have very similar feeding characteristics. These six species could have been lumped into one 'species'. Clearly, simulations removing species will yield different results with different decisions regarding resolution. Ideally, a food web should show interactions among different trophic species, functional groups of taxa that share the same set of predators and prey within a food web. The trophic species is a widely accepted convention in structural food-web studies that reduces methodological biases related to uneven resolution of taxa within and among food webs (Williams & Martinez 2000).

Invasion by plants causes the greatest secondary loss of species, which is cascading and quite substantial for the rainforest. Caveats made above regarding the loss of basal species with nutrient enrichment also apply here.

6.4.6 Changes to food web topology with social impact

Sections 6.4.2-5 have simulated a selection of removal sequences representing different sources of social impact. This section summarises the results, comments on the insights that topological network analysis might provide in predicting future ecosystem states, and identifies issues that require further research.

Social predation led to substantial negative changes in connectance, although the severity of impact depended on how many species were removed. Topological network analysis leads to the conclusion that the robustness of ecosystems in which multiple species are subject to overharvesting is threatened. Regime shifts following secondary extinctions and food web fragmentation are likely, and this likelihood increases as more species are exploited and species richness declines. The main issue requiring clarification is whether targeted species are highly-connected. This has been my assumption, and while it seems plausible, needs corroboration. Topological network analysis treats neither interaction strength, nor the existence of top-down or bottom-up controls on populations. While important information, it is often difficult to obtain. I conclude that topological network analysis is a potentially useful tool for assessing ecosystem responses to heavy social predation.

Bioaccumulation was shown to cause connectance to decline, indicating robustness was adversely affected. Vulnerable species to this source of social impact tend to be top predators, or at least higher order consumers. However the main topological effect of their loss is compaction of the food web. There are few secondary losses. The reason for this is that secondary loss occurs primarily through the loss of food sources, while this removal sequence results in the loss of predators. Without secondary losses, ecosystem states are more likely to change as a result of changes in top-down controls on intermediate feeders, which topological network analysis does not simulate. Consequently, I judge topological network analysis of limited use for assessing ecosystem responses to bioaccumulation.

Topological network analysis is a poor tool for assessing ecosystem responses to nutrient enrichment, invasion by a plant species, or any source of social impact that results in the loss of basal species. Because my topological approach deals with the presence or absence of interaction, and not its strength or the amount of energy transferred, it may indicate greater robustness than would be the case in reality.

Habitat loss and fragmentation bears some similarities to bioaccumulation. Vulnerable species tend to be large-bodied top predators and their loss leads to food web compaction. However, the potentially large number of removals with habitat loss, in comparison with bioaccumulation on top predators that affects only a handful of species, means that this form of social impact can effect substantial changes to food web topology. This loss is exacerbated, as demonstrated for the rainforest food web, by the loss of large-bodied vertebrates that are secondary consumers and the prey of other secondary consumers. A high degree of interconnectedness among secondary consumers means that secondary loss and fragmentation might yet occur. I assess topological network analysis as being potentially useful in cases of habitat loss, and highlight two areas where additional information is needed.

The first is identification of the species most vulnerable to habitat loss. While literature was cited in Section 6.3.4 to support the approach taken above, there is a contrary view, espoused by Holling (1992), which argues for intermediate consumers rather than top predators. This view is controversial, and I chose not to review the quite substantial literature treating it. However, if Holling is correct, the impact on food web topology could be severe as highly-connected species tended to be intermediate consumers in both food webs simulated above.

The second is the issue of the relationship between habitat and species loss, not only whether it is linear but also whether the line passes through the origin.

Finally, topological network analysis indicated that biotic exchange could cause species loss and establish new hubs. However, our constrained understanding of the shift from introduced to invasive makes it uncertain that topological network analysis will contribute to our management of this form of social impact. Its use in explaining and analysing the observed effects of invasion can be envisaged. However its use in predicting future ecosystem states is dependent on assumptions as to which species are vulnerable to extinction.

6.5 Socio-natural networks

6.5.1 Introduction

Coevolution is driven by interaction. Interaction may trigger adaptation, although my analysis focuses on the failure of organisms to adapt, or extinction. Adaptation and extinction will affect other components in the larger network of interactions in which they participate. Adaptation or extinction of marginal players can be expected to cause only a ripple as a result of small changes in network structure. On the other hand, adaptation or extinction of key players may cause a cascade that may produce substantial change in network structure and the state of the system.

This chapter has focused so far on the left-hand side of Figure 6.1. More realistic protocols for species removal have been simulated, introducing the social system but only as a source of impact. Loss of species from ecosystems and fragmentation of ecological networks as a result of social impact may rebound on social networks. By extending the network to include the social, and particularly economic, network that uses an ecosystem, the potential exists to assess reciprocal effects. It is also possible that existing network representations from social systems could be extended to include ecological networks, for the same purpose. This section addresses how interactions among components of both systems could be represented and what, if any, methodological issues need to be resolved in their linkage. I focus on food webs, representing ecological networks, and the economy, representing social systems.

The previous section and Chapter 5 have used predation matrices as the means of mapping interactions in a food web and simulating species loss. The predation matrix documents the presence or absence of a feeding interaction between pairs of species, with the species on the row consumed (or not) by the species on the column. This approach has strong parallels with the input-output (I-O) table used in macroeconomic analysis. The two techniques are compared in Section 6.5.2. The possibility of extending each to encompass interactions with and within the other system is addressed in Section 6.5.3. Methodological issues are discussed in Section 6.5.4.My method for assessing coevolution, specifically for assessing impacts on the robustness of socio-natural networks, is then outlined in Section 6.6.

6.5.2 Parallels between predation matrices and the input-output table

An I-O table attempts to record all transactions associated with economic activities. It forms the basis for I-O models (developed by Wassily Leontief 1936; 1941; 1966), the supply and use tables within the Social Accounting Matrix (SAM) and the System of National Accounts (SNA) from which such macroeconomic aggregates as Gross National Production and National Income are derived. The structure of an I-O table is shown in Figure 6.6. Cell entries depict production by the rows and consumption by the columns. In economics, consumption equals use; production is defined as all goods and services that are intended to be sold at the market or used by a production unit itself, as well as goods and services produced by the government and non-profit organisation with paid employees (UN 1993).

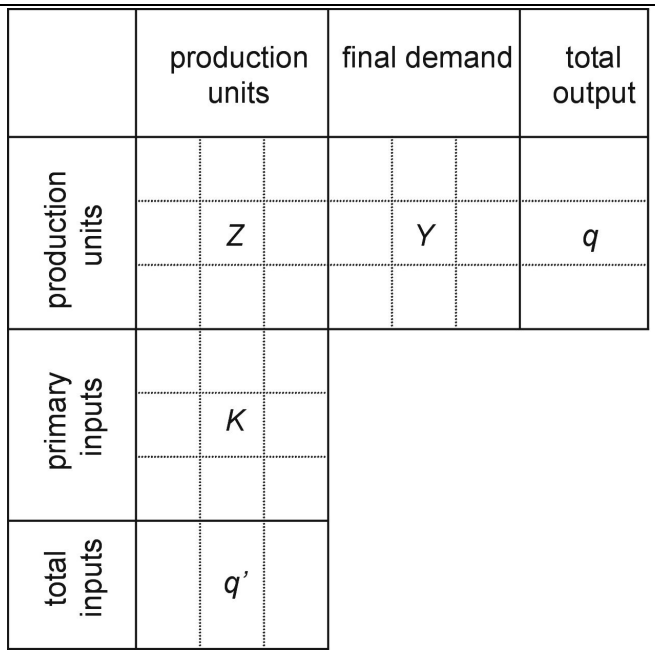


Figure 6.6 An input-output (I-O) table

Some inputs to production units are purchased from other production units, and these are represented by matrix *Z* in Figure 6.6. Two main types of production units may be identified: industries – organisational units of the economy that undertake production; and commodities – goods and services produced. Cell entries in this matrix, z_{ij}, document how much output from industry *i* is used as input to the production processes of industry *j*, or how much of commodity *i* inputs to the production of commodity *j*. A predation matrix may be seen as an ecological equivalent of the inter-industry form of the *Z* matrix. Cell entries in a predation matrix, p_{ij}, show that the production of species *i* contributes to the production of species *j*. Here production refers to that part of the assimilated food or energy that is retained and incorporated in the biomass of an organism (Allaby 1998).

While the predation matrix captures feeding interactions among the components of a food web, the forms seen so far in this dissertation capture only the presence, not the quantity, of matter and energy transfers. Further, food webs components tend to be distinguished taxonomically, as has been seen particularly for the El Verde rainforest, and not functionally. The ecological equivalent of an industry is the trophic species, func-

tional groups of taxa that share the same set of predators and prey within a food web. The trophic species is a widely accepted convention in structural food-web studies that reduce methodological biases related to uneven resolution of taxa within and among food webs (Williams & Martinez 2000).

Trophic species and industries are parallel concepts. Industries are distinguished by their production processes, which determine both their inputs and their outputs. Trophic species are often taxonomically similar. They are distinguished by the species they consume and the species that consume them; that is, by their inputs and outputs. In specifying production units or trophic species for the construction of an I-O table or a predation matrix, choices are made with regards the level of detail. This level of detail is termed resolution by ecologists. The choices tend to be a compromise between classification systems (largely taxonomic in ecology, sectoral in economics) and data availability.

A major difference between the predation matrix and the *Z* matrix is that the former documents only matter flows. I-O tables trace financial flows of both goods and services. The flows of goods through economies parallel matter flows through ecological communities. As yet, an ecological equivalent to the provision of services has not been examined, although Section 6.2 introduced the notion of engineering networks. Niche construction may be seen as a service provided by one species to another.

There are many similarities between an I-O table, although primarily the inter-industry *Z* matrix, and a predation matrix. System components are distinguished on the basis of similar inputs and outputs, and cell entries document interactions between pairs of components. There are two main structural differences. Firstly the I-O table incorporates the strength of the interaction, usually expressed in monetary units. Secondly the I-O table includes flows of services as well as of goods.

6.5.3 Capturing interactions within and between the two systems

This section examines the possibility of capturing all interactions within and between an ecosystem and an economy in one format. In other words, whether I-O analysis can be extended to include interactions in ecological communities, or whether predation matrices could be extended to include economic interactions. The inclusion of all interactions in one ‘super’ matrix would facilitate tracing of reciprocal effects of species loss on both systems. I term the network represented by such a super matrix a ‘socio-natural network’. It subsumes interactions within the individual networks of the social and natural systems, as well as socio-natural interactions between the two systems.

I-O analysis, which uses all of the matrices in Figure 6.6, is a powerful analytical tool in macroeconomics. One of its many advantages is that is not restricted to monetary units. I-O tables may be constructed in physical units (e.g. Dorfman *et al*. 1958) and even in mixed physical and monetary units (e.g. Leontief & Ford 1972; Ayres & Gutmanis, 1972; James *et al*. 1983). Consequently it is possible to include matter flows from ecosystems into and through the economy, and so include interactions between the two systems within the I-O format. However complete interlinkage of ecological and economic I-O matrices, encompassing interactions within and between both systems, is not yet possible, and arguably not desirable. This is due to incompatibilities in data availability and spatial scale.

While there is a growing database of food webs, it has yet to include the volume of biomass or energy transfer from one species to another. Mass balances for only a very limited number of food webs exist, such as in applications of the Ecopath software (http://www.ecopath.org/). Data collection supporting the construction of I-O tables is in place in most nations, and to the extent that I-O tables are constructed regularly, often annually. A comparable capacity for ecosystems is not yet possible.

I-O tables are usually constructed for national economies. Full representation of interactions between and among economic and ecological systems means the construction of predation matrices for all ecosystems within national borders. Not only is this a potentially large number of ecological communities, but national borders also tend not to correspond with ecosystem boundaries. Consequently there is a mismatch of spatial scales in combining the two at the national level. There is also the question of aggregation. Would the effects on a single ecosystem of species loss, and subsequent effects on dependent economic actors, be discernable in such an aggregate matrix?

Environmental management tends to occur at smaller spatial scales, often a compromise between administrative, such as local or state government, and natural boundaries, such as a coastal zone, an estuary, a forest, or a river catchment. Given the growing database on food webs and ecological literature in general, the construction of predation matrices at such spatial scales should be possible. I-O tables can be construction at sub-national levels but pose problems for the spatial disaggregation of national economic data and in the specification of imports and exports. Construction of sub-national I-O tables requires considerable data processing.

Incompatibilities in data and spatial scale mean that the extension of I-O tables to incorporate ecosystems is not yet feasible. The conversion of an I-O table to the predation matrix format, where only the presence or absence of interaction is indicated, is a relatively simple process. I propose to extend predation matrices to include not only humans, a species which should appear in many ecological networks anyway, but more specifically human activities.

6.5.4 Methodological issues in extending a predation matrix

Three issues for the extension of a predation matrix are identified. The first is resolution. Humans could easily appear in food webs as just another trophic species. However such an approach would provide little information about social networks. We have seen with I-O analysis above that different human activities may be distinguished with different inputs and outputs, just as trophic species may be distinguished on the basis of prey and predators. It is interaction among production units that form the basis of economic networks. Only some of these production units interact directly with trophic species in a food web, but others may be dependent on such interaction. The extension of a predation matrix via production units and using industry classification systems would yield a representation a socio-natural network with relatively consistent resolution of nodes.

The second issue is the type of interaction. Food web analysis is guided by principles governing the conservation of mass and energy, although predation matrices are only approximate in how they conform to these principles. Wastes, such as carbon dioxide, organic waste and heat are not specifically treated, although categories such as detritus are

regularly included (e.g. the ECOWeB database of Cohen 1989; Cohen *et al*. 1990). Food web analysis has generally not directed equal attention to return flows of wastes and detritus as it has to flows to higher trophic levels, although this situation is changing (e.g. Neutel 2001; Neutel *et al*. 2002). Detritivore food chains tend to be underrepresented, usually because the species involved are small and poorly distinguished taxonomically. Small organisms, and particularly simpler life forms such as bacteria and viruses, are rarely included despite suspicions that they play a major role in many ecological communities (e.g. viruses may influence ecological dynamics and biogeochemical cycling in ocean ecosystems – IMBER 2005).

Unlike predation matrices, I-O is very rigorous in its adherence to accounting principles, in a sense the 'conservation of money'. The sum of the inputs to production units equals the sum of outputs; the vector *q'* in Figure 6.6 is the transposed vector of *q*. The usefulness of I-O in economic analysis and in national accounting lies in this rigour. However, there is also much to criticise (e.g. various contributions to Ahmad *et al*. 1989). I highlight two aspects.

Firstly, I-O pays little attention to principles of conservation of mass and energy. As a result, flows of residuals from sectors and households into the environment are generally ignored. Secondly, not all economic transactions occur at formal markets. Many environmental goods and services are not traded formally, and so do not appear in an I-O table. This implies that, for example, removal of wastes by rivers has no value. There are also production units that do not operate in formal markets, such as the production, distribution and sale of illegal substances. This point is relevant to the case study in the following chapter, where a stand of mangroves supports a largely subsistence economy.

I-O tables document financial flows associated with the exchange of goods and services between production units. Goods comprise matter and energy. Predation matrices map only the flow of matter and energy. Services, such as the provision of habitat via niche construction, are not included. Networks involving the exchange of services between organisms clearly exist, but their representation is complicated by the absence of a 'currency' for the transaction. For internal consistency, the extension of a predation matrix to economic interactions is better confined to interactions involving the transfer of matter and energy.

The third methodological issue is that of spatial extent, particularly given the mismatch discussed above. Neither I-O tables nor predation matrices are explicit with regards to spatial character of their components. I-O tables require specification of spatial extent, usually national borders. Predation matrices are constructed for an ecosystem, but the bounds of ecosystems can be quite arbitrary, in part due to their tendency to grade into one another, and in part determined by research focus and data collection. Until there is better understanding of the implications of aggregating predation matrices, I argue for a focus be on management issues dealing with single ecosystems and their users.

6.6 Topological network analysis of socio-natural

The purpose of this chapter was to move from the largely theoretical approach in Chapter 5, towards applying topological network analysis to environmental management. To this end, I have:

- identified species most at risk of extinction from social predation;
- assessed the topological effects on two food webs of species removals that better reflect social impact;
- compared the predation matrix, which forms the basis of topological network analysis, with the input-output table, which presents similar information but for an economy; and,
- examined the extension of I-O tables and predation matrices to incorporate interactions with and within the other system.

More realistic removal protocols

Topological network analysis assesses the impact on network topology of species loss. Prior to this chapter, protocols for species removal have been based on connectedness. There is no *a priori* reason why a species' connectedness should be linked to its extinction risk. However it is possible that connectedness is related to, or dovetails with, other ecological characteristics of species. Some authors have argued that the keystone function of species could be defined in terms of connectedness. That highly-connected species play a crucial role in network topology and robustness is clear. However, highly-connected does not necessarily mean keystone, at least according to the current definition of keystone. More research is needed to understand better the ecological significance of being highly-connected.

Much of this chapter is devoted to specifying the species at risk of extinction from social impact, assessing their position and connectedness in ecological networks, and simulating their loss from the St. Marks seagrass and El Verde rainforest food webs. The literature was used to identify species at risk. The translation of risk to position and connectedness is approached using a series of assumptions. A selection of social impacts, based on these assumptions, have been simulated. These simulations indicate the potential threat to networks from social impact, as well as the potential usefulness of topological network analysis for indicating the risk of change in an ecosystem's state.

Topological network analysis shows potential for indicating regime shifts caused by social predation and habitat loss and fragmentation. Social predation on multiple species in a food web leads to a removal protocol that is similar to, but not as extreme as, removing the most highly-connected species. Our capacity to drive multiple species close to extinction, through harvesting, could very well cause reduced food web robustness and lead to ecosystem instability. The main economic activity that targets multiple species in an ecosystem is fishing. The robustness of aquatic ecosystems may be under threat, and not just because individual stocks being overfished. However my assumption that the targeted species are highly-connected needs verification.

Based on a literature review, I argued that size, taxonomy and trophic level determine species' vulnerability to habitat loss and fragmentation. Removal of large-bodied, higher order vertebrates, particularly from the rainforest food web, caused large declines in connectance, indicating substantial decline robustness. Apart from verifying my assumption regarding vulnerability, further research is needed in specifying the species-area relationship of ecosystems with area loss.

Topological network analysis is considered to have less potential for assessing the effects of emissions and biotic exchange. Emissions can lead to a potentially wide range of effects on network topology. If my assumption holds that direct toxic effects are likely to affect sensitive, poorly-connected species, far-reaching consequences for ecological networks are unlikely unless many species are lost. Bioaccumulation tends to affect the fitness of top predators and their loss leads to compaction of the food web. While negative changes to connectance indicate reduced robustness, network compaction is more likely to affect the community via changes in predator control that is not reflected in changes to network topology.

Topological network analysis was shown to be of little use for assessing social impacts that affect competitive balances among basal species, as occurs with eutrophication and invasion by exotic plants. The loss of basal species can be simulated, but since they are often dominant species used to identify ecosystems – seagrass, rainforest, but also mangrove, grassland – there loss leads to apparently trivial but quite fundamental questions such as "when is a forest no longer a forest". Is it sensible to assess the impact on a forest of removing the trees? These issues highlight that topological network analysis is static, whereas the processes resulting in species loss are dynamic.

Finally, a selection of possible instances of biotic exchange was simulated. I judge topological network analysis to be of limited predictive capacity in such instances. There are, potentially, an infinite number of ways in which new species enter food webs and this constrained my analysis of the addition of species in Chapter 5. It is then very difficult to generalise what the impacts on network topology might be. Certainly more information is needed on changes in the pattern of interaction strengths as well as of interactions themselves. However my simulations offer descriptive insights, particularly in the way certain patterns of invasion result in new hubs. The documentation of invasions using a network approach might serve to provide insights into the invasive process and its consequences.

The next chapter presents a case study in which I demonstrate how topological network analysis could be applied to the management of an ecosystem facing the possibility of (further) habitat loss.

A socio-natural network

In developing more realistic protocols for species loss, I have shown the potential usefulness of topological network analysis in assessing ecological network robustness and the potential for regime shifts in ecosystems when an ecosystem is subject to social impact. By extending the network to include the social, and particularly economic, network that uses an ecosystem, the potential exists to assess reciprocal effects. However, it is also possible that existing representations of social networks could be extended to include ecological networks.

Input-output tables and predation matrices have much in common. Both adopt a functional approach to identifying system components, although I-O is much more rigorous in this. Both document flows from one component to another, that result from interaction. I-O does this rigorously in accordance with accounting principles. I-O is less rigorous in terms of the types of interactions it captures; while documenting both goods and

services, it focuses almost exclusively on those transacted via formal markets. Predation matrices may, one day, rigorously follow principles for the conservation of mass and energy. For the moment, this is not possible and only the presence of an interaction leading to the transfer of matter can be documented.

While it is possible to extend I-O tables to include flows of matter and energy from ecosystems into and through economies, it is not possible to extend this further into ecological systems and so capture all interactions among components. However, it is possible to adopt the predation matrix approach and apply it to economic systems. Three methodological issues were discussed for such an approach, leading to the following recommendations:

- care with resolution in specifying components of economic and ecological systems is needed, based on the definition of the trophic species and systems classification of production units;
- only interactions that result in a flow of matter and energy from one components to another are documented; and,
- initially the focus is small scale, lying with the management of single ecosystem and the local economy dependent on it.

Topological network analysis estimates changes to the pattern of interactions among the components of a system, and interprets the changes in terms of impacts on the network's robustness. A decline in robustness indicates reduced stability that, in turn, indicates an increased likelihood that the systems will undergo a state change. Implications for robustness are drawn from three factors, two of these being fragmentation and secondary node loss since they are used to define robustness. The third is change to connectance, which was examined in Chapter 5.

Topological network analysis applied to a socio-natural network, encompassing all interactions within and between natural and social systems, would enable assessment of the reciprocal effects on the two systems of species loss. This is undertaken in the next chapter.

7. Coevolution, Socio-natural Networks and Mangrove Management

"Gods tend to be interested in prophets, not profits."

"Going Postal", Pratchett 2005, p 387

7.1 Introduction

Topological changes to a socio-natural network, representing interactions among the components of both a social and a natural system, could provide insights into the future coevolution of these systems and of the sustainability of development. They could support managers in their choice of action by providing information on: the likelihood of abrupt changes in system performance because the network fragments, loses nodes secondarily, and/or other effects on network robustness. These are aspects of coevolution that have been investigated in the previous chapters, and now will be investigated in the context of ecosystem management for sustainable development. The research question is: could changes in network topology provide insights into the repercussions of different human interventions in an ecosystem?

This chapter reanalyses research conducted during the 1990's to demonstrate how topological changes to a socio-natural network might provide management insights. Gilbert and Janssen (1998) examined the impacts of changing the management of the Pagbilao mangroves in the Philippines. The mangroves were being preserved, but there was considerable pressure on those responsible for managing natural resources to permit conver-

sion to fishponds or some other economic use. Mangroves throughout the world are still under pressure from conversion (UNEP-WCMC 2006). Gilbert and Janssen's approach addressed the sustainability of development by designing interventions into the mangroves that were economically sustainable and that ensured the continued provision of environmental services (e.g. clean water, nursery functions, flood mitigation) by the mangroves. These services are provided almost exclusively by the complex root systems of mangroves. Consequently our approach assumed that economic sustainability plus sustained mangrove viability equals sustainable development. It falls under 'weak sustainability' in that it permits substitution between natural and man-made capital. I highlight four constraints to o earlier approach.

Firstly, it does not guarantee the viability of the mangrove ecosystem, only of the mangroves. If natural capital is taken to be the ecosystem and not just its predominant species, then the analysis falls short of sustainable development.

Secondly, we highlighted the possibility of irreversible biodiversity loss, and viewed biodiversity as an important component of the decision problem. Such loss refutes the assumption of substitution between human and natural capital. However this was ignored due to uncertainties and knowledge constraints.

Thirdly, we assumed essentially linear relationships, such as between mangrove cover and ability to provide environmental services. Thresholds and non-linearities in mangrove performance could not be included due to lack of information, even though they were considered very likely. Such uncertainty and unpredictability was attributed to the high degree of interconnectedness within the ecosystem and among the various bay ecosystems.

Fourthly, ecological information does not always fit well within economic analysis. While our valuation study made a step towards integration by attempting to take environmental functions into account, these aspects were addressed less rigorously than economic goods for which values could be determined. The integration of information from the natural and social systems centred on the mangroves remained partial.

My application of topological network analysis addresses these constraints directly. A network representing interactions among components of the mangrove ecosystems and the local economy captures both biodiversity and interconnectedness. I do not distinguish between the natural system, i.e. the mangrove ecosystem, and the social system, i.e. the local economy. I focus on components of the two systems and on their interactions. My approach makes no assumption regarding linearity, nor about substitutability between different forms of capital. The sustainability criterion for comparing interventions draws from coevolutionary thinking – unsustainable development compromises the robustness of an existing pattern of socio-natural interactions.

My method and this chapter follow four steps illustrated in Figure 7.1. Section 7.2 describes the study area, options for human intervention, and summarises Gilbert and Janssen's earlier analysis. Section 7.3 develops the reference socio-natural network (Step 1), mapping interactions among the mangrove community and mangrove users. The interventions involve the entry of new economic activities. In network terms, this means the addition of new nodes and links to the reference network, as indicated in Step 2 and detailed in Section 7.4. New activities and uses of the mangroves mean the loss of habi-

tat, and in turn, the loss of species. The precise relationship between habitat and species loss is unknown for the Pagbilao mangroves. Step 3, in Section 7.5, derives a plausible relationship and specifies how many, which, and in what order species will be lost.

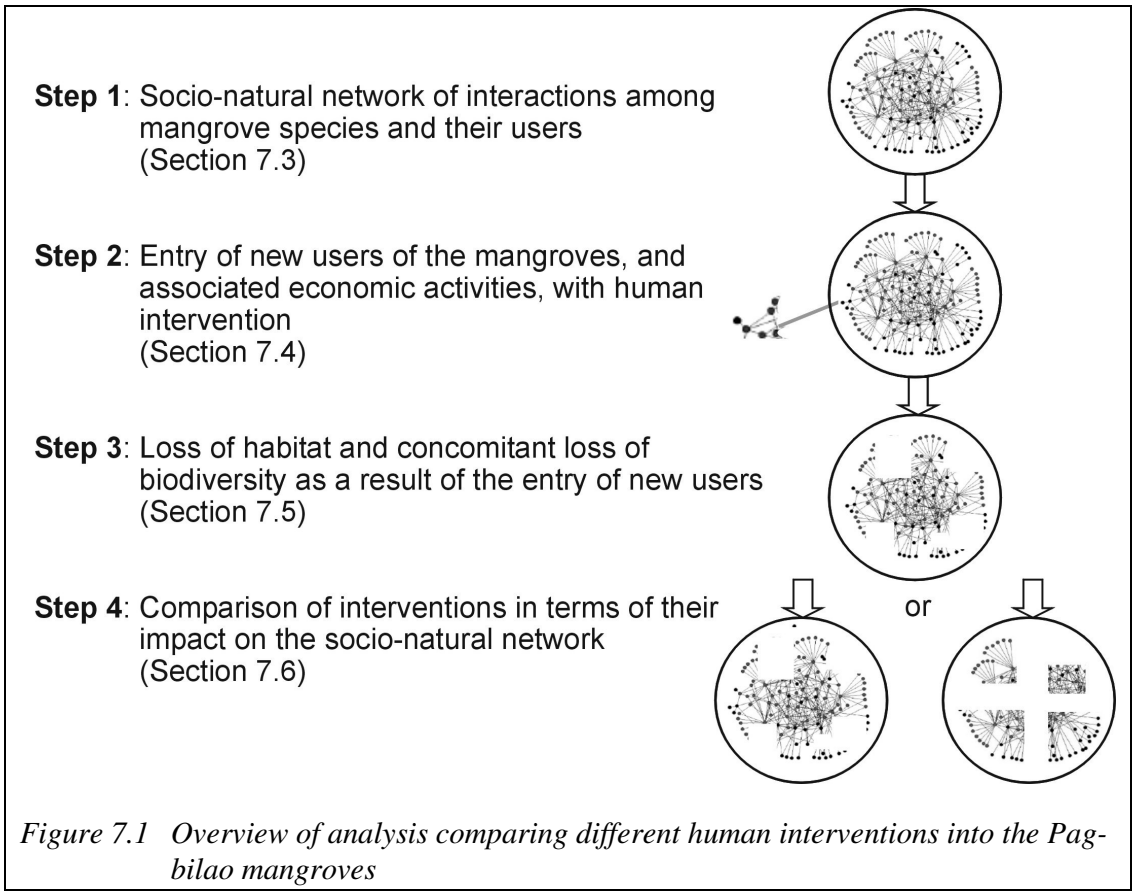


Figure 7.1 Overview of analysis comparing different human interventions into the Pagbilao mangroves

Robustness has been previously defined in terms of the propensity of networks to fragment and/or to lose nodes secondarily. Chapter 5 also showed that changes in connectance could indicate impacts on robustness. In contrast to Chapter 5, where similar protocols of node loss were used to compare the robustness of different networks, Section 7.6 compares the effect of different protocols on the same network. Performance of interventions is measured, and the interventions ranked in terms of secondary node loss, fragmentation, and connectance change, to capture the threat posed by each intervention to the reference network's robustness.

By comparing interventions, insights for management are derived and are discussed in Section 7.7. Section 7.8 concludes the chapter. Further reflections on my analysis may be found in Chapter 8.

7.2 The Pagbilao mangroves – conversion or preservation?

7.2.1 The study area

The municipality of Pagbilao is located on the island of Luzon, the Philippines (see Figure 7.2). Pagbilao Bay is separated from the larger Tayabas Bay by an island, Pagbilao

Grande, and by coral reefs. Pagbilao Bay and its mangroves are listed among wetland areas with high conservation priority (Scott & Poole 1989; Ong *et al*. 2002; DENR 2003).

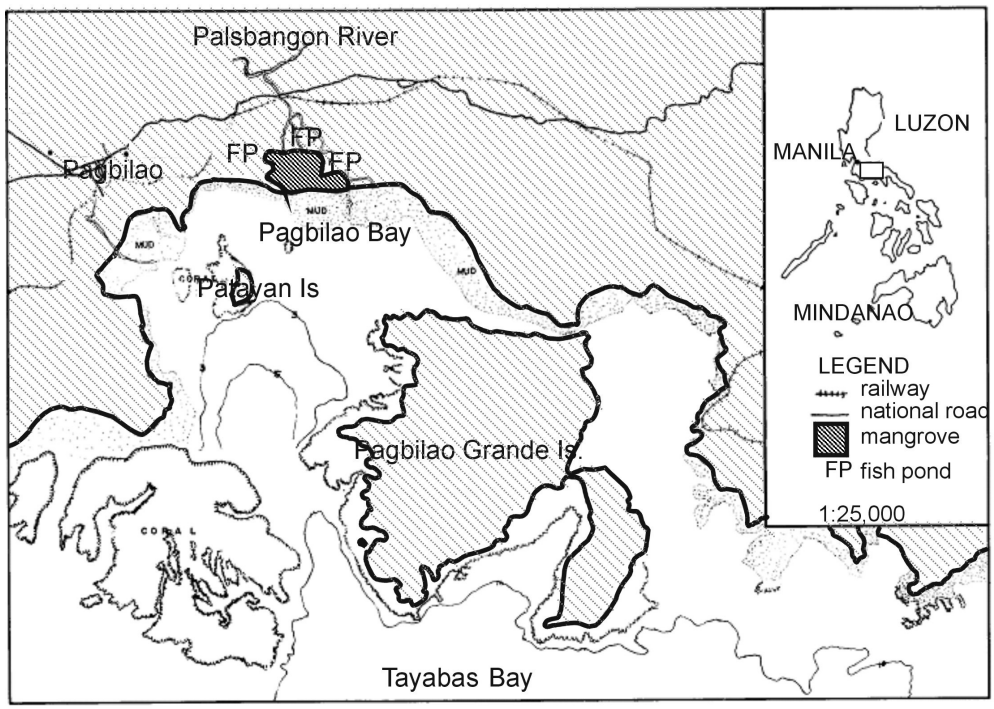


Figure 7.2 Pagbilao Bay and the Pagbilao mangroves

Mangrove stands and fish catches in the Philippines have declined (Calumpong 1994; Figure 7.3). The original area of mangroves is unknown but probably extended beyond the current stand to include adjacent fishponds (see Figure 7.2). The total area of mangroves was around 700 ha in 1984. Only 111 ha – the Pagbilao mangroves – remain.

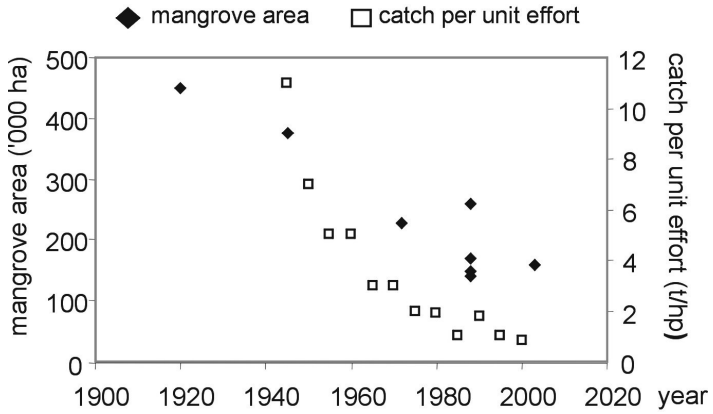


Figure 7.3 Estimated mangrove area (DENR 2003) and catch per unit effort measured in tons per size of motor (Melana et al. *2000) in the Philippines*

The stand was cut in the 1970's for commercial fuel wood and charcoal, and so is second growth. It comprises 19 species of mangroves (56% of all true mangroves), the largest number for any stand in the Philippines. It is the also the most diverse (Arroyo 1979); National Resources Management Center 1980). The dominant mangrove species are *Rhizophora apiculata*, *R. mucronata*, *Ceriops tagal*, *C. decandra*, *Avicennia officinalis*,

A. marina, *Excoecaria agallocha* and *Bruguiera cylindrical* (Bennagen & Cabahug 1992). Figure 7.4 shows part of the stand, comprising *Rhizophora* and *Nipa* palm.

Figure 7.4 Pagbilao mangroves seen from the mouth of the Palsabangan River

The Pagbilao mangroves have been declared an experimental forest under the jurisdiction of the Department of Environment and Natural Resources. The legal basis lies with Presidential Proclamations 2151 and 2152, which declare parts of the Philippines to be wilderness areas as of 1981. These laws withdraw a large portion of mangrove areas from entry, sale, settlement and other forms of disposition. Local communities have traditionally used the mangroves for a variety of products. While cutting down trees has been prohibited since 1981, branches may be cut for fuel or for construction purposes. Illegal cutting of boles occurs (personal observation 1996; Carandang & Padilla 1997). Various leaves, fruit, flowers and fungi may be taken to prepare traditional medicines. The coastal villages of the bay are dependent on fishery resources, and also collect edible shells and crabs from the mangroves. Commercial trawling is prohibited, and so the catch is taken using artisanal techniques such as corrals, traps, and hooks and lines.

Fishpond development began in the 1980's. Mangrove strips were kept to stabilise the embankments surrounding the ponds (see Figure 7.5). Aquaculture development was exclusively the monoculture of milkfish (*Chanos chanos*) by extensive or semi-intensive means (Padilla & Tanael 1997). Wealthy individuals, who neither live in the area nor employ local residents to manage them, own the ponds. The trend in the Philippines is towards more intensive aquaculture – higher stocking density, more frequent cropping, use of artificial feeds, fertilisers and pesticides (Padilla & Tanael 1997). The remaining stand of mangroves is under pressure for conversion to aquaculture.

Increasing awareness of the ecological importance of mangroves led to the establishment of a mangrove nursery at the edge of the stand in 1977. Mangrove propagules are collected, established at the nursery, and exported for mangrove afforestation projects throughout the Philippines. The stand is close to four universities. Scientists and students are common visitors for research and education purposes.

Figure 7.5 Fishponds adjacent to the Pagbilao mangroves

7.2.2 The different human interventions

Current management of the Pagbilao mangroves is based on preservation. A number of human interventions can be envisioned, involving new uses of the mangroves and entry of new economic activities into the area. I examine eight interventions based on forestry and/or aquaculture as new uses of the mangroves. Interventions differ in terms of the mix of uses, the products and practices used to generate products, as well as different amounts of habitats loss. The interventions are summarised in Table 7.1. The two small-scale aquaculture interventions were not included in the earlier analysis.

Each intervention is paired with conditions ensuring the sustainability of new economic activities and the supply of environmental services by the mangroves. The sustainability conditions focus on maintaining viable mangroves with their complex root systems that underlie many environmental services. Part of the analysis tested the failure of sustainability conditions. More information on the interventions and sustainability conditions may be found in Gilbert and Janssen (1998).

Table 7.1 Different human interventions in the Pagbilao mangroves

	Products and practices	Impact on mangrove habitat
PR	Minor products collected by locals	None
SF	Wood for local use	Harvesting based on 30 years recovery.
CF	High value wood products	Harvesting based on 30 years recovery.
SA-1	Semi-intensive milkfish culture	65% mangroves retained as buffer zones.
SA-2	Semi-intensive milkfish culture	35% mangroves retained as buffer zone.
IA-1	Alternating extensive milkfish and intensive shrimp culture	65% mangroves retained as buffer zone.
IA-2	Alternating extensive milkfish and intensive shrimp culture	35% mangroves retained as buffer zone.
SF/IA	Extensive milkfish and intensive shrimp culture with wood for local use	30% converted to fishponds; harvesting of remainder based on 30 years recovery.
CF/IA	Extensive milkfish and intensive shrimp culture with high value wood products	30% converted to fishponds; harvesting of remainder based on 30 years recovery.

PR	Preservation
SF	Subsistence forestry
CF	Commercial forestry
SA-1	Semi-intensive aquaculture, small scale option
SA-2	Semi-intensive aquaculture, large scale option
IA-1	Intensive aquaculture, small scale option
IA-2	Intensive aquaculture, large scale option
SF/IA	Subsistence forestry/intensive aquaculture
CF/IA	Commercial forestry/intensive aquaculture

7.2.3 The provision of mangrove goods and services

Would conversion of the mangroves to economic use derive more value from the mangroves? Gilbert and Janssen's analysis identified mangrove goods and services and estimated their values per intervention (see Table 7.2). The aquaculture alternatives in this table correspond with the large scale options in Table 7.1. Values could be expressed in monetary units for most goods; services could only be valued qualitatively.

Table 7.2 shows that semi-intensive aquaculture has the highest economic value. Environmental services need to be priced very highly for Preservation or a forestry intervention, which score well on environmental values, to achieve a higher total value. The literature did not support such high values. A sensitivity analysis on the sustainability conditions showed that semi-intensive aquaculture ranks highly except with the most pessimistic view. The analysis supports conversion of the mangroves to semi-intensive aquaculture. However, and as argued by Gilbert and Janssen, the valuation approach excluded management-relevant information, such as irreversible biodiversity loss. The appropriateness of valuation to support decisions involving irreversible effects was challenged.

Table 7.2. Net annual value (10^3 US$) from the Pagbilao mangroves, under different human interventions (Gilbert & Janssen 1998)

	PR	SF	CF	SA	IA	SF/IA	CF/IA
Goods							
Fisheries	6.6	6.4	6.4	0.32	0.3	1.6	1.6
Subsistence wood	0	14.0	0	0	0	7.6	0
Commercial wood	0	0	16.64	0	0	0	9.2
Aquaculture - fish	0	0	0	752.0	543.1	199.7	199.7
Mangrove nursery	+	+	+	0	0	0	0
Total goods	**6.6**	**20.4**	**23.08**	**752.4**	**543.4**	**208.8**	**210.4**
Services							
Aquaculture waste	0	0	0	++	+++	++	++
Damage control	+++	+++	+++	+	+	++	++
Ecotourism	+++	++	0	0	0	+	0
Existence value	+++	++	++	0	0	+	+
Information value	+++	+++	++	0	0	+	+
Total services	**+++**	**+++**	**++**	**+**	**+**	**+**	**+**

PR	Preservation	+++	large contribution to value
SF	Subsistence forestry	++	moderate contribution to value
CF	Commercial forestry	+	small contribution to value
SA	Semi-intensive aquaculture	0	no contribution to value
IA	Intensive aquaculture		
SF/IA	Subsistence forestry/intensive aquaculture		
CF/IA	Commercial forestry/intensive aquaculture		

7.3 A socio-natural network based on the Pagbilao mangroves

7.3.1 Introduction

This section constructs the reference socio-natural network. This network captures existing interactions among the various actors associated with the Pagbilao mangroves, and precedes human intervention. The network takes the form of an extended predation matrix, documenting the presence or absence of interaction among 88 nodes. Nodes are either trophic species from the mangrove ecosystem or production units from the local economy. Production units are identified on the basis of consuming the same inputs and delivering outputs to the same consumers, drawing on the notion of the trophic species, which consume the same prey and are consumed by the same predators. As with the predation matrices in Chapter 5, the presence of interaction between nodes is given by a cell entry of '1' and it shows the transfer of matter and energy from the node on the row to the node on the column. How much matter and energy is transferred is not indicated.

As shown in Figure 7.6, the network comprises two sub-networks: the predation matrix documents feeding interactions among mangrove inhabitants (hence the stylised *Rhyzophora* mangrove tree overlaying this matrix); and, the economic matrix documents interactions involving production units, including the extraction of goods from the mangroves and subsequent transactions of these goods among production units.

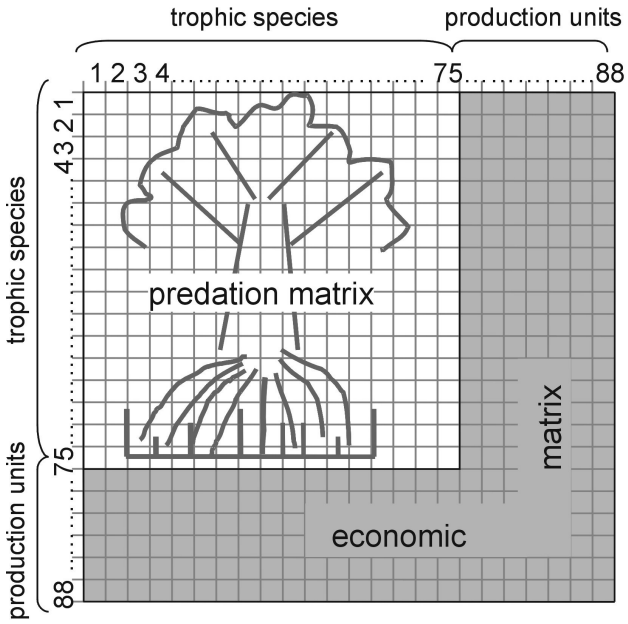


Figure 7.6 The reference socio-natural network for the Pagbilao mangroves

Interaction between trophic species and production units removes organisms from the ecosystem. These goods may ultimately leave the area (e.g. export of the crab, *Scylla serrata* to the Manila fish markets), contribute to local production activities (e.g. wooden stakes holding feed bags in ponds), or be consumed by the local community (e.g. fungi used to make medicines). Sections 7.2.3-4 detail construction of these matrices.

7.3.2 The predation matrix

A literature and internet search yielded pictorial representations of mangrove food webs and three predation matrices. The latter, forming part of the ECOWeB database in Cohen *et al*. (1990), relates to mangroves in Hawaii and consists of 8, 9 and 22 trophic species. The pictorial representations, such as Figure 7.7, were generally no larger. As discussed in Chapter 5, food webs consisting of so few species present problems for analysis.

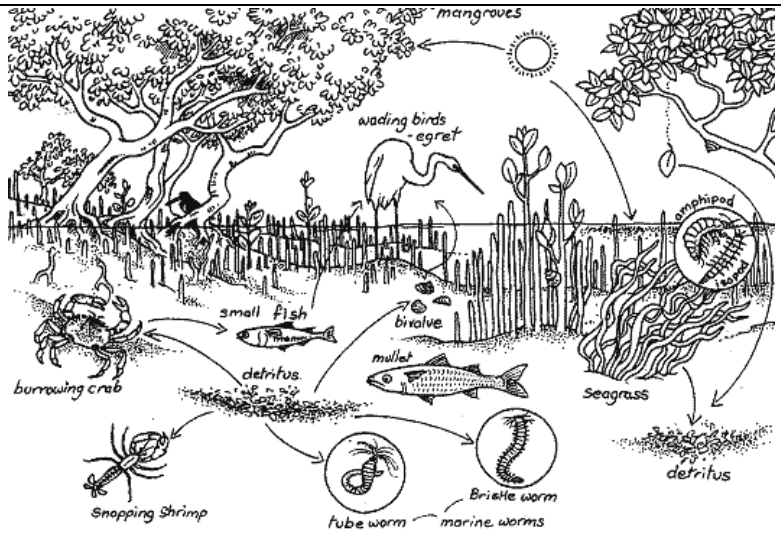


Figure 7.7 A mangrove food web (http://www.mesa.edu.au/habitat/chall04.asp#top)

Food webs from the literature focused on part of the mangrove ecosystem – the aquatic/littoral component. Mangroves also comprise an arboreal component, above the water line with species living in and around the leaves, branches and stems. Their exclusion is inconsistent for my purposes as local human use of the mangroves includes such species.

I have based my predation matrix for the Pagbilao mangroves on the predation matrices of the St. Marks seagrass and El Verde rainforest food webs, seen in Chapter 5. They were taken as proxies for the aquatic/littoral and arboreal components respectively. Aggregating rainforest species to create trophic species reduced large differences in resolution between the two matrices. Construction of the predation matrix was supplemented by other sources of information viz.:

- species lists from the Pagbilao mangroves (chapters and background documents of Janssen & Padilla 1997, http://www.arcbc.org.ph/; http://www.birdwatch.ph/);
- literature discussing feeding relationships in mangrove communities (e.g. Cohen *et al*. 1990; Amblers & Alcala-Herrera 1994; Sheridan 1997; Primavera 1998; Lee 1999; Macintosh *et al*. 2001; Bouillon *et al*. 2002; Thimdee *et al*. 2004);
- internet sites providing food preferences for fish found in the mangroves (e.g. http://www.fishbase.org, http://marinefisheries.org);
- expert knowledge (Carandang 1996, pers. comm.; Guarin 1996, pers. comm.; Ong 1996, pers. comm.; Vermaat 2003, pers. comm.).

The result is a set of 75 nodes (trophic species) encompassing both the aquatic/littoral and arboreal components of Pagbilao mangroves (see Table 7.3). The former component is more diverse. No literature was found on trophic links between the two components. A small number of such links involve species found in both components. This is one area where further research is needed. The predation matrix for the Pagbilao mangroves comprises nodes 1 to 75 of the network in Appendix I. Appendix II lists the full set of network nodes (i.e. trophic species and production units) and their identification codes.

Mangroves are obviously the predominant, but not the only, basal species of the predation matrix. With a focus on trophic species, 17 basal species were identified encompassing plant parts (e.g. flowers, roots), epiphytes, plant associates, algae, phytoplankton, detritus and dead wood. Primary consumers correspond approximately with the St. Marks seagrass and El Verde rainforest webs. A number of species from the seagrass food web, notably herbivorous ducks and brittle stars, were excluded because they are not found in mangroves. Two nodes were added to accommodate sessile organisms such as oysters (*Ostrea orientalis*, *O. palmipes*) and barnacles (*Balanus sp*.), attached to mangrove roots. The 40 primary consumers from the rainforest web were aggregated into six nodes, distinguished by size and prey. Species from the rainforest found in soil and freshwater communities were excluded.

Of the 86 secondary consumers from the rainforest, some do not occur in Pagbilao such as mongoose and poisonous frogs). The remainder were condensed into 12 nodes distinguished by size and taxonomy. Secondary consumers for the aquatic/littoral component were taken from the seagrass food web, with the exception of one shrimp and nine fish nodes identified from species lists (Janssen & Padilla 1997; http://www.arcbc.org.ph). Their food preferences were derived from Cohen *et al*. (1990), http://www.fishbase.org and http://marinefisheries.org. These ten nodes are distinguished by food preferences and life history, such as permanent or transient residence of the mangroves.

Table 7.3 Trophic species for the Pagbilao predation matrix

Trophic level	Aquatic/littoral component	Arboreal component
Basal	mangrove roots	plants
	mangrove seeds and seedlings	live leaves
	micro-epiphytes (including algae)	live wood
	macro-epiphytes	sap
	benthic algae	pollen
	phytoplankton	nectar
	detritus	fruit
		flowers
		lichens
		dead wood
Primary Consumers	benthic bacteria and fungi	fungi
	microfauna	insects on flowers and fruit
	meiofauna	insects on leaves
	microprotozoa	other herbivorous insects
	zooplankton	fruit-eating birds
	epiphyte-grazing amphipods	fruit-eating bats
	isopods	
	suspension-feeding molluscs	
	small filter feeders on hard surfaces	
	large filter feeders on hard surfaces	
	epiphyte-grazing gastropods	
	deposit-feeding polychaetes	
	suspension-feeding polychaetes	
	small, largely herbivorous shrimps	
	deposit-feeding peracaridan crustaceans	
	hermit crabs	
	spider crabs (herbivores)	
Secondary Consumers	predatory shrimps	(ecto)parasites
	omnivorous crabs	insectivorous insects
	mud crabs	insectivorous bats
	predatory gastropods	spiders[1]
	other gastropods	other arthropods[1]
	predatory polychaetes	insectivorous birds (1)
	fish feeding on epifauna	rat
	ovivorous and planktivorous fish	small lizards
	resident carnivorous fish	insectivorous birds (2)
	gobies	large lizards and small snakes
	milkfish (juvenile)	insectivorous birds (3)
	herbivorous fish	big arthropods[1]
	mullet (juvenile)	
	juvenile piscivorous fish	
	resident piscivorous fish	
	juvenile shrimp (penaeids)	
	benthos-eating birds	
	fish and crustacean-eating birds	
	fish-eating birds	
	gulls[2]	
Top Predators		raptors[2]
		owls
		snakes

1 These three trophic species are mutually exclusive.

2 Trophic species feeding in both components of the ecosystem.

Three top predators were identified. The predation matrix has a standardised connectance of 0.049. A uniform function best fits the degree distribution ($r^2 = 0.96$). However an F test comparing uniform, exponential and power law fits showed that there was no significant difference ($p < 0.05$) between the uniform and exponential fits, but significant differences between these two and a power law fit.

7.3.3 The economic matrix

The economic matrix documents social predation on a number of species from the mangroves and their subsequent transaction. The matrix is confined to activities within the Pagbilao municipality. Thirteen production units (IDs 76-88, Appendix II) from three current uses of the mangrove – artisanal fishing, extensive aquaculture and collection – are identified. Figures 7.9-7.11 show nodes and links associated with each use.

Artisanal fishing takes marine species from the mangroves and the bay. This activity is split into two nodes based on technique, species taken, and catch destination. Artisanal fishing (bay) uses larger equipment in open water and catches larger species. The more valuable part of this catch is sold to a buyer for the Pagbilao fish market (see Figure 7.8). The most lucrative species is a crab, *Scylla serrata,* taken from mud flats bordering the mangroves. The buyer sells to various vendors at the Pagbilao market who, in turn, sell to local hotels and restaurants, local communities, and buyers for the Manila markets.

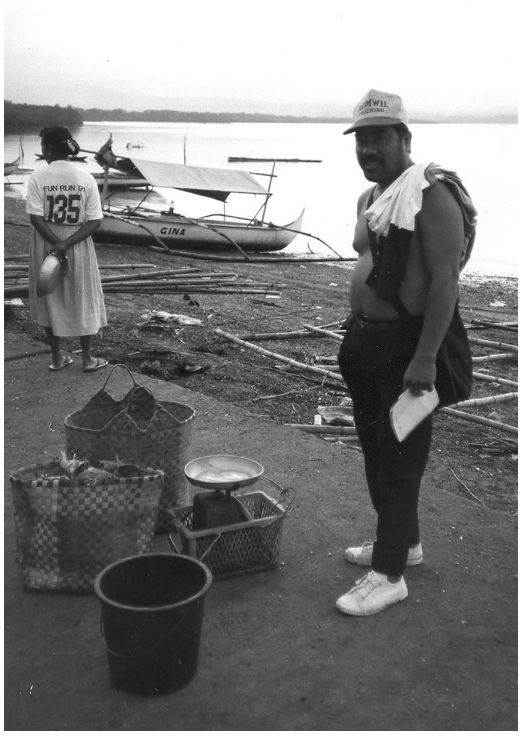


Figure 7.8 Buyer for the Pagbilao fish market purchases from a local fisherman

Artisanal fishing (mangrove) uses less and smaller equipment that can be used in the confined spaces of the mangroves. The catch is small-sized, comprising mangrove residents and juveniles of bay species. It is traded within the local community or destined for own consumption. The various production units and transactions associated with ar-

tisanal fishing are depicted in Figure 7.9. Both fishing activities generate detritus (via cleaning fish), which feeds back to the predation matrix.

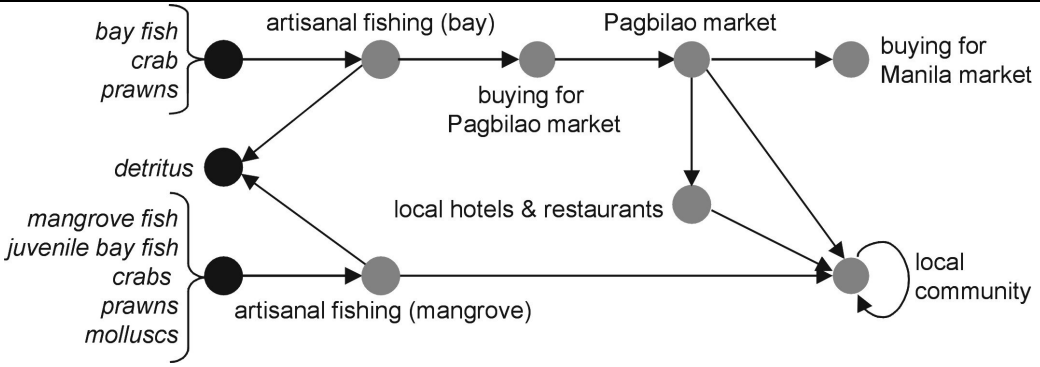


Figure 7.9 Artisanal fishing (bay and mangrove) and nodes that exchange fishing products; black nodes denote trophic species from the predation matrix; artisanal fishing feeds back to the predation matrix via detritus

Extensive aquaculture uses the mangroves as a source of wood. Juvenile stock is caught elsewhere, neither in the mangroves nor in the bay. Live wood is used for construction purposes, such as the stakes holding artificial food dispensers. Dead wood is used for fuel. The product of aquaculture is sold to a buyer for the Manila fish market who exports it from the study area; aquaculture products do not appear at the Pagbilao fish market. Aquaculture also caters for two feedbacks to the predation matrix. The first is organic wastes from the fish and surplus fish food, which enter the mangroves when the ponds are flushed. They contribute to detritus. The second occurs when individuals escape from the ponds. These interactions are depicted in Figure 7.10.

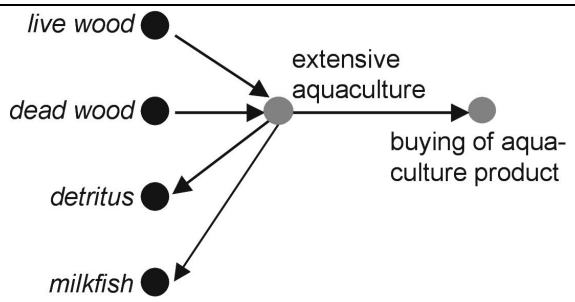


Figure 7.10 Extensive aquaculture and production unit that takes its product to the Manila markets; black nodes denote trophic species from the predation matrix; aquaculture returns detritus and captured species to the predation matrix

Local inhabitants collect various species from the mangroves. I distinguish two collecting activities (see Figure 7.11). Elderly individuals, women and children collect minor mangrove products such as: edible marine snails, oysters and other molluscs; leaves for thatching; dead wood for fuel; fungi, flowers and plant parts for traditional medicines; and mangrove seeds and seedlings. The mangrove seeds and seedlings are established by a mangrove nursery located in the mangroves, then exported for transplantation in mangrove afforestation and reafforestation programs throughout the Philippines. Other collected goods are for own use or exchanged within the local community. Stronger members of the local community collect larger products, mainly live wood such as branches,

Nipa shingles and mangrove boles (technically illegal) for construction purposes, and larger items of dead wood for fuel. Both collecting activities may contribute to detritus.

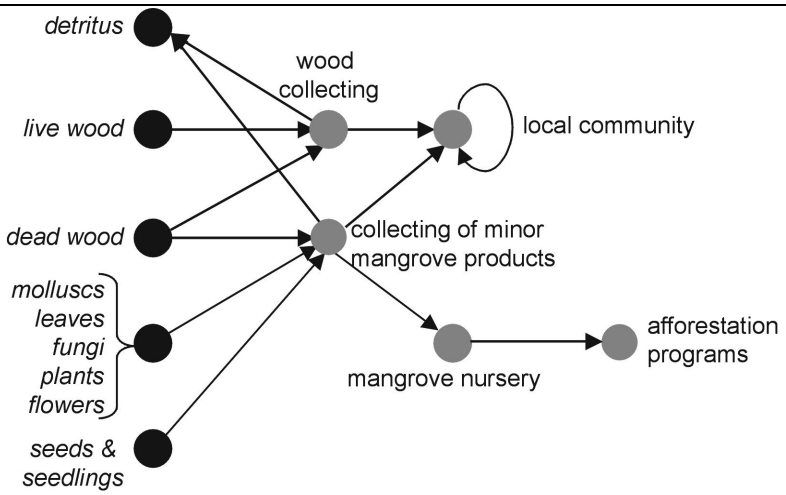


Figure 7.11 Collection and transaction of wood and minor mangrove products; black nodes denote trophic species from the predation matrix; collection feeds back to the predation matrix via detritus

The economic matrix is characterised by product chains rather, and has a low standardised connectance of 0.013. Best fit for the degree distribution is an exponential function ($r^2 = 0.91$), although an F-test showed that there is no significant difference among uniform, exponential and power law functions.

7.3.4 The Pagbilao socio-natural network

The reference socio-natural network for the Pagbilao mangroves is presented in Appendix I. The network records the presence or absence of interaction among 88 nodes; 75 are trophic species and 13 are production units. Cell entries of '1' indicate a flow of matter and energy from row to the column; blank cells indicate no flow. Nodes are listed in Appendix II. The socio-natural network has a standardised connectance of 0.040. Best fit for the degree distribution is a uniform function ($r^2 = 0.97$), although an F-test showed that there is no significant difference from an exponential function. The F-test also showed that these fits are significantly different from a power law function ($p<0.5$).

7.4 Entry of new economic activities

The addition of new nodes representing new economic activities is discussed in this section. Each intervention adds at least one new production unit and at least one new link to the socio-natural network. The new production unit may replace an existing unit, and it may cause the loss of existing interactions. These changes are shown per intervention in Figures 7.12-16. Grey nodes represent new production units. Black nodes are a part of the reference network. Black nodes labelled in italics are trophic species. Stippled nodes and lines indicate nodes and links respectively that are lost with entry of the new production unit(s). Nodes or links unaffected by an intervention are not shown.

7.4.1 Forestry (SF and CF)

Two forestry interventions are considered. Subsistence forestry exploits the mangroves for live and dead wood; the local community uses the products (see Figure 7.12). Subsistence forestry replaces 'wood collecting' and introduces two production units to bring the goods to a distribution centre that would become the local source of wood products.

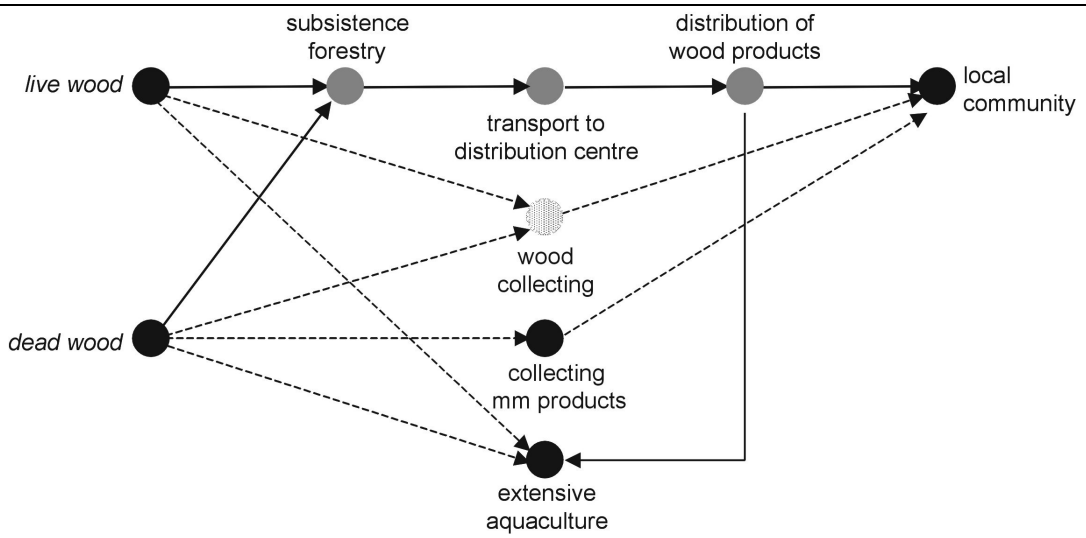


Figure 7.12 Subsistence forestry and nodes transacting its products; black nodes are from the reference network; stippled nodes and lines indicate nodes and links that are lost – wood products will be obtained directly from a distribution centre

Commercial forestry extracts high value wood products (see Figure 7.13). It adds three production units required to generate and process product and transport it to markets outside the area. Commercial forestry would only use live wood from the boles of trees and larger branches. Smaller branches would not be used, and so could be collected from forestry sites; this creates new links to existing live wood users. The entry of commercial forestry will make no change to the collection of dead wood from the mangroves. As a result, wood collecting is not lost with this option as it is with subsistence forestry.

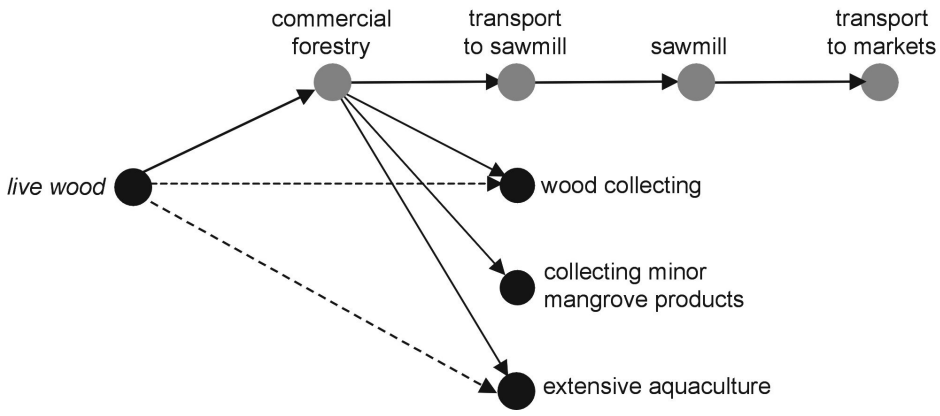


Figure 7.13 Commercial forestry and nodes transacting its products; black nodes are from the reference network; stippled lines indicate links lost with entry of commercial forestry –wood products will be obtained from forestry sites

7.4.2 Aquaculture (SA-1, IA-1, SA-2, IA-2)

Four aquaculture interventions are examined, each adding only one node corresponding to the new form of aquaculture. Aquaculture product is sold to buyers from the Manila markets, which is an existing node in the network. The new production unit uses wood from the mangroves, and feeds back to the predation matrix via the escape of stock species. While semi-intensive (SA) and intensive (IA) aquaculture differ in terms of technique and product, they differ only by one link in the network (see Figure 7.14) through the escape of prawns into the bay. SA-2 and IA-2 differ from SA-1 and IA-1 only in converting a larger area of mangrove to fishponds.

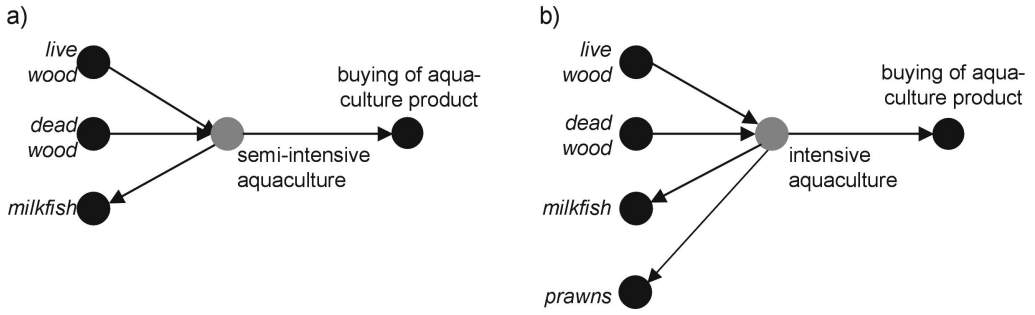


Figure 7.14 Aquaculture: a) semi-intensive SA-1 and SA-2, b) intensive IA-1 and IA-2; black nodes indicate nodes from the reference network

7.4.3 The combined interventions (SF/IA and CF/IA)

The remaining interventions combine each of the two forms of forestry with intensive aquaculture, as shown in Figures 7.15 and 7.16.

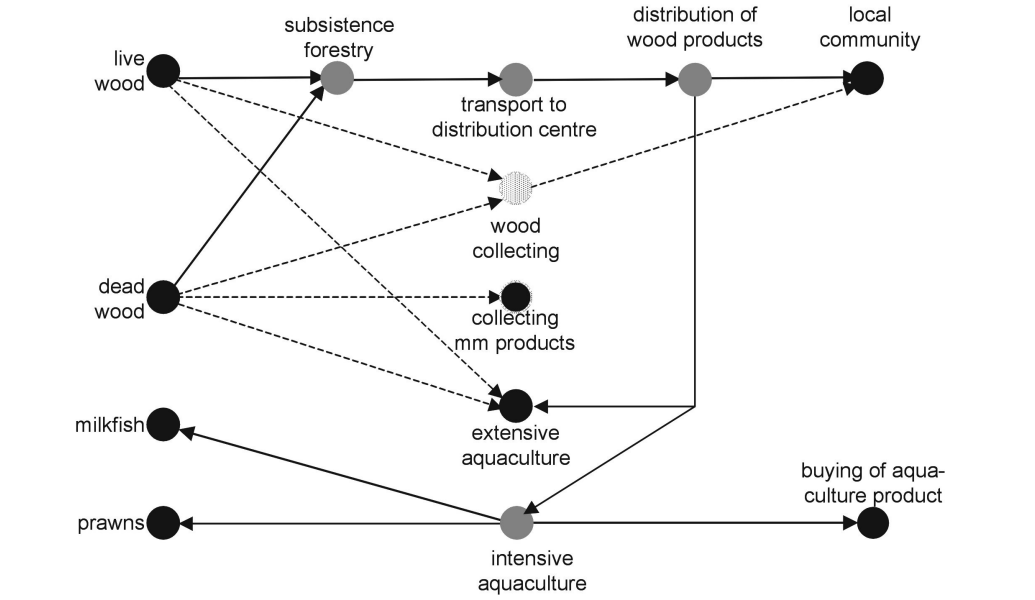


Figure 7.15 Subsistence forestry and intensive aquaculture (SF/IA); black nodes are from the reference network; the stippled node and lines indicate nodes and links that are lost because wood products are obtained directly from a distribution centre supplied by subsistence forestry

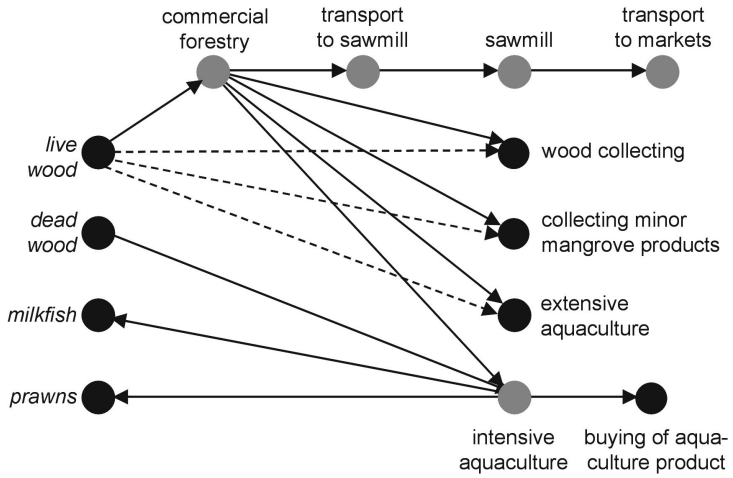


Figure 7.16 Commercial forestry and intensive aquaculture (CF/IA); black nodes are already present in the reference network; the stippled lines indicate links that are lost with the entry of commercial forestry as wood collecting and aquaculture derive their live wood needs from forestry sites

7.5 Impact on biodiversity

7.5.1 Introduction

The entry of new production units results in the loss of mangrove habitat. Part of the mangroves are either replaced by fishponds, or removed as wood products. As discussed in Chapters 2 and 6, loss of habitat leads to loss of species. The third step in my analysis specifies the impact that new production units can be expected to have on biodiversity and develops protocols for removing species from the reference socio-natural network. Specifically, it identifies how many species are to be removed from the network per intervention, and in what order. This in undertaken in four steps:

1. classification of trophic species according to their vulnerability to habitat loss;
2. estimation of the amount of habitat loss per intervention;
3. specification of the relationship between habitat loss to species loss for the Pagbilao mangroves; and
4. identification of how many and which species are lost, and in which order.

7.5.2 Which species are vulnerable to habitat loss?

The Pagbilao mangroves are the remains of a once larger stand. Loss and fragmentation of mangrove habitat has been taking place at least over the last 30-40 years and have already contributed to local biodiversity loss. For example, the Philippines monkey (*Macaca philippinensis*) is now locally extinct. The mangroves are also a crucial stepping-stone in bird migration paths (e.g. Brahminy kite, *Haliastur indus*, and shorebirds, herons and egrets such as *Egretta garzetta*, *E. alba* and the endangered *E. eulophotes*). Mangrove loss could be expected to cause increased mortality in these populations (Ong 1996, pers. comm.; http://www.arcbc.org.ph/wetlands/philippines/phl_tayabas_bay.htm).

The following discussion classifies the trophic species from the predation matrix into ten categories of increasing vulnerability to habitat loss. The ten categories comprise: one of

ubiquitous species, three of basal species and close associates, three of invertebrates, and three of vertebrates (see Table 7.4).

Table 7.4 Vulnerability categories (VC), from 1=least vulnerable to 10=most vulnerable, for trophic species from the Pagbilao predation matrix

VC	ID	Trophic species
1	15	benthic algae
	16	phytoplankton
	17	detritus
	19	benthic bacteria & fungi
	23	zooplankton
	63	rat
	71	fish-eating birds
	72	gulls
	74	owls
2	1	mangrove roots
	5	live wood (including *Nipa*)
	12	dead wood
3	2	mangrove seeds & seedlings
	3	plants
	4	live leaves
	6	sap
	7	pollen
	8	nectar
	9	fruit
	10	flowers
4	11	lichens
	13	micro-epiphytes
	14	macro-epiphytes
	18	fungi
	27	small filter feeders on hard surfaces
	28	large filter feeders on hard surfaces
5	20	microfauna
	21	meiofauna
	22	microprotozoa
	24	epiphyte-grazing amphipods
	25	isopods
	36	insects on flowers & fruit
	37	insects on leaves
	47	(ecto)parasites
6	26	suspension-feeding molluscs
	29	epiphyte-grazing gastropods
	30	deposit-feeding polychaetes
	31	suspension-feeding polychaetes
	38	other herbivorous insects
	46	predatory polychaetes
	50	spiders
	51	other arthropods
	32	herbivorous shrimps
	33	deposit-feeding peracaridan crustaceans
	34	hermit crabs
	35	spider crabs
7	41	predatory shrimps
	42	omnivorous crabs
	43	mud crabs
	44	predatory gastropods
	45	other gastropods
	48	insectivorous insects
	61	shrimp (transient)
	68	big arthropods
8	39	fruit-eating birds
	40	fruit-eating bats
	49	insectivorous bats
	52	fish feeding on epifauna (resident)
	53	ovivorous and planktivorous fish (resident)
	54	carnivorous fish (resident)
	55	gobies (resident)
	56	milkfish (transient)
	57	herbivorous fish (resident)
	58	mullet (transient)
	59	piscivorous fish (transient)
	60	piscivorous fish (resident)
	62	insectivorous birds (1)
9	64	small lizards
	65	insectivorous birds (2)
	66	large lizards
	67	insectivorous birds (3)
	75	snakes
10	69	benthos-eating birds
	70	fish and crustacean-eating birds
	73	raptors

The first category comprises species that would be present whether the mangroves were or not, and so is the category least vulnerable to mangrove loss. It comprises aquatic species typical of the larger bay environment, and terrestrial species that use the mangroves for only part of their total habitat and food requirements. The former tend to be small, ubiquitous organisms, viz. benthic algae, phytoplankton, detritus, benthic bacteria and

fungi and zooplankton. The latter are mobile and relatively large, viz. owls, fish-eating birds (that also take fish from the ponds, at considerable risk), gulls and rats.

All interventions were designed so that mangroves would continue to be viable and to provide environmental services, notably shoreline stabilisation and flood mitigation. These services are a function of mangrove root systems and, to a lesser extent, of their trunks and branches. Consequently the next least vulnerable category comprises mangrove roots, live and dead wood. The third category comprises other plant parts – flowers, pollen, leaves, etc. The fourth category consists of trophic species in close association with mangrove roots and wood, and includes basal species (micro- and macro-epiphytes) as well as fungi and littoral species that use mangroves as substrate.

In Chapter 6 it was argued that the most vulnerable species to habitat loss and fragmentation were the larger vertebrates from higher trophic levels. The vulnerability of the remaining trophic species is distinguished on the basis of size, taxonomy, and trophic level. The largest vertebrates in higher trophic levels, viz. benthos-eating and fish and crustacean-eating birds and raptors, are the most vulnerable (category ten). These trophic species include migratory birds identified mentioned above as being vulnerable to the loss of the Pagbilao mangroves. The next most vulnerable category (9) comprises large reptiles, including a top predator, and other large birds from the arboreal component of the mangroves. Category eight comprises the remaining vertebrates. Categories five, six and seven are inverterbrates, distinguished by size. Category five comprises small invertebrates, largely herbivores living in close association with basal species. The sixth category comprises the larger epifauna, benthic species and the remaining herbivorous insects. The seventh category comprises the largest invertebrates.

No distinction of species' vulnerability is made within each of these ten categories. The removal protocol removes all trophic species within a vulnerability category, beginning with category 10 and moving progressively through less vulnerable categories, until the specified number of removals has been reached.

7.5.3 How much habitat is lost?

Loss of habitat for the aquaculture interventions is specified in Table 7.1. Habitat loss from forestry is less straightforward. The anticipated forestry technique is selective logging on a 30-year rotation, assumed to be sufficient to allow for full recovery of habitat and regrowth of timber. Habitat is also lost in providing support for forestry operations, such as access roads and stockpiles. In such a small stand (111 ha), these sources of habitat loss could to be disproportionately large.

I have estimated habitat loss based on clear felling, rather than selective logging. Under clear felling, all trees within a designated area, or coup, are removed; the coup is not harvested again until it has regenerated. Assuming 30-year rotation, a coup harvested in year 1 will be harvested again in year 31. Habitat recovers between the end of year 1 and the beginning of year 31, so over a period of 29 years. Clear felling means that all mangrove habitat in a coup is lost. Habitat loss during the first 30-year rotation is given by:

$$HL_n = \frac{n}{30} - \left(\frac{1}{30} \sum_{i=1}^{n} \frac{i-1}{29} \right) \qquad \text{Eq. (7.1)}$$

where
HL_n = total fraction of habitat area lost by year n; and,
n = any year within the first 30-year rotation.

The first term in this equation captures habitat loss in year n, always one-thirtieth of the total area. The second term represents habitat recovery, and is assumed to be linear. In year 1 of the first rotation, one-thirtieth (3%) of habitat is lost and there is no recovery. In year 4, say, four-thirtieths (13.3%) of habitat has been lost, but the coups harvested in years 1-3 inclusive have partially recovered; the net loss of habitat in year 4 is 12.6%.

Figure 7.17 plots net loss of mangrove habitat over the first 40 years of forestry operations, and shows that a steady state is reached at the end of the first rotation; loss and recovery are equal, and net loss is 50%. Consequently, I assume that the forestry interventions cause loss of 50% of habitat.

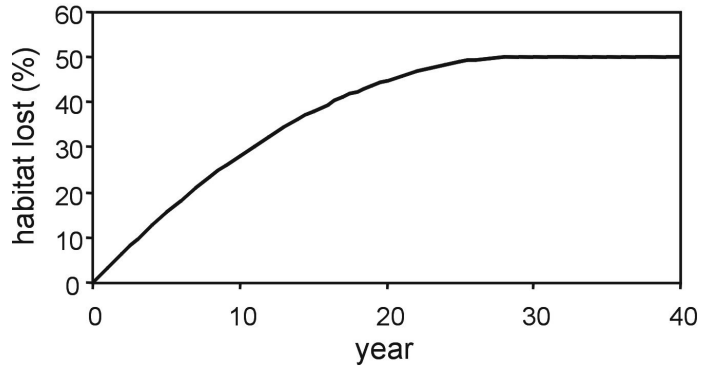


Figure 7.17 Net loss of mangrove habitat, expressed as a fraction, due to forestry operations

7.5.4 How many species are lost?

This section relates mangrove habitat loss to species loss. Figure 2.2 depicts the conventional view of how species numbers increase with habitat expansion and decline with habitat contraction. As discussed in Chapter 6, there is evidence to suggest a linear relationship between species loss and habitat loss, so that the exponent z of the Species Area Relationship equals 1. This leads to the following equation:

$$S_l = cA_l \qquad \text{Eq. (7.2)}$$

where
S_l = fraction of species lost; and,
A_l = fraction of habitat area lost.

The issue becomes the value of c, or the slope of the line. Three options are illustrated in Figure 7.18, which plots species loss against habitat loss. Intuitively, there would be no species lost if no habitat were lost and all species would be lost if all habitat were lost. This leads to the middle line. However, the discussion on vulnerability above identified a number of species found in the Pagbilao mangroves that are likely to persist even with total mangrove loss. Generalists and species drawing from a range of habitats would seem capable of surviving this habitat's loss. This suggests the lower line in Figure 7.17, with some proportion of species remaining when all habitat is lost. However, the con-

verse can also be argued – no species remain after habitat declines below a threshold or minimum critical area (upper line).

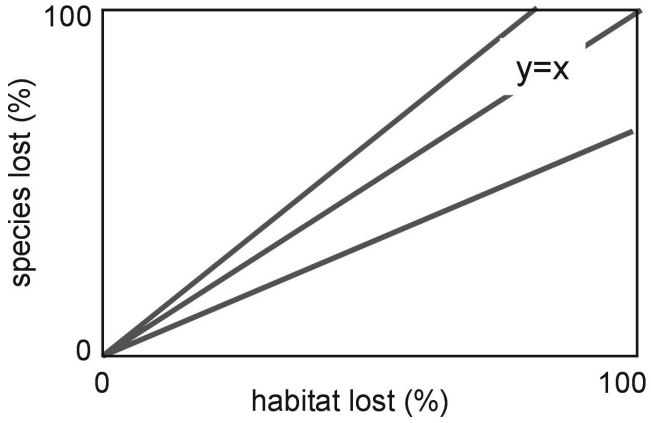


Figure 7.18 Possible relationships between species and habitat loss

Selecting the most appropriate relationship for the loss of mangrove habitat is complicated by two further factors. Firstly, mangrove habitat has already been lost, and so presumably species as well. Past losses cannot be quantified, and so it is not possible to determine where the mangroves are currently situated relative to 'pristine' conditions. Secondly, my predation matrix tracks trophic species and not taxonomic species. Trophic species is a functional definition, focusing on feeding rather than on reproductive isolation. The SAR addresses taxonomic species, despite our inability to distinguish all organisms in a food web to the species level. To illustrate, of the 44 insect 'species' listed in the El Verde rainforest food web, only two are identified at the species level.

I have chosen to assume a linear relationship as the best approximation of the relationship between mangrove habitat loss and trophic species loss. Further, I assume that the loss of *x%* of mangroves leads to the loss of *x%* of trophic species excluding those species in vulnerability category 1. For the 66 species vulnerable, to some degree, to habitat loss, their loss may be expressed as:

$$S_l = 66A_l \qquad \text{Eq. (7.3)}$$

where

S_l = number of species lost; and,

A_l = habitat lost expressed as a fraction of total, initial habitat of 111 ha.

7.5.5 Species lost per intervention

Habitat loss per intervention has been estimated in Section 7.5.3. Equation 7.3 estimates the number of species lost as a result of habitat loss. The most vulnerable categories of species are lost first. The current situation, Preservation, loses neither habitat nor species. Table 7.5 tracks, per intervention (first column), habitat loss (second column), total species loss (third column), vulnerability categories lost and order of loss (fourth column), to primary removals of species (last column). The third and fifth columns are not exactly the same because species within vulnerability categories are removed simultaneously – there is no distinction among species within a category. Fewer species are often removed

primarily than specified by Equation 7.3. Removal of a further vulnerability category exceeds the required species loss, and this allows for some secondary loss of species.

Table 7.5 Proportion of habitat and trophic species lost per interventions

Intervention[1]	Mangrove lost (%)	No. species to be removed[2]	Vulnerability categories and order of removal	Primary removal of species
SF	50	33	10, 9, 8, 7	29
CF	50	33	10, 9, 8, 7	29
SA-1	35	23	10, 9, 8	21
SA-2*	65	49	10, 9, 8, 7, 6, 5	49
IA-1	35	23	10, 9, 8	21
IA-2*	65	49	10, 9, 8, 7, 6, 5	49
SF/IA	30 (fishponds) + 35 (forestry)	49	10, 9, 8, 7, 6, 5	49
CF/IA	30 (fishponds) + 35 (forestry)	49	10, 9, 8, 7, 6, 5	49

1 See table 7.1 for key to abbreviations
2 From Equation 7.3

Species losses occur primarily and secondarily. Primary removal means species are lost as a direct effect of habitat loss. Secondary loss means loss of connection to the network, usually because the network provides it with no matter or energy.

7.6 Impact of different human interventions

7.6.1 Introduction

Available evidence suggests that there have been no major changes in environmental or economic performance in the study area over the last 30 or so years. I take this as evidence that the current situation, Preservation, has a reasonably robust socio-natural network. Aquaculture began in the 1970's. To date, it has not had the adverse environmental impacts seen in other parts of Asia (e.g. Lin 1989; Naylor *et al*. 1998; Paez-Osuna 2001). Secondary growth has taken place since harvesting for charcoal, and has led to an apparently viable ecosystem. Overharvesting of bay and mangrove species, particularly fish and crabs, is the most likely source of declining environmental and economic performance.

Beginning with the reference network developed in Section 7.3 and representing Preservation, my analysis simulates intervention as changes to the network. One or more new production units enter the network, cause loss of mangrove habitat, and subsequently loss of trophic species. Sections 7.4 and 7.5 identified the number of production units and links to be added to the network and the number and order of species to be lost.

The final step compares interventions with regards to their effects on the robustness of the Pagbilao socio-natural network. I assess these effects via three criteria: 1) fragmentation; 2) secondary node loss; and 3) changes to network connectance. Robustness is de-

fined in terms of the first two criteria. Chapter 5 showed that reduced robustness could be paired with changes in a network's connectance, particularly sharp negative changes.

The results per intervention are summarised in Table 7.6 and discussed in Sections 7.2.2 and 7.3.3. The current situation, Preservation, is not included in Table 7.6; continuation of the current situation is assumed not to change the network. The table highlights performance on the three criteria, but also provides additional information. The interventions are ranked in Section 7.2.4. A sensitivity analysis is conducted in Section 7.2.5.

Table 7.6 Summary of the impact of interventions on the socio-natural network

	Intervention[1]							
	SF	CF	SA-1	IA-1	SA-2	IA-2	SF/IA	CF/IA
Fragmentation	no	no	no	no	no	no	no	no
Total 2^{ndry} node loss	6	6	0	0	8	8	8	8
Trophic species lost	30	30	21	21	43	43	43	43
- primary removal	29	29	21	21	41	41	41	41
- secondary loss	1	1	0	0	2	2	2	2
Production units lost	5	5	0	0	6	6	6	6
- primary removal	0	0	0	0	0	0	0	0
- secondary loss	5	5	0	0	6	6	6	6
ΔC_{stand}	-0.021	-0.021	-0.017	-0.017	-0.026	-0.026	-0.028	-0.028
$\% \Delta C_{stand}$	53	53	43	43	65	65	70	70
Initial[2] ΔC_{stand}	-0.002	-0.003	-0.001	0.000	-0.001	0.000	-0.003	-0.004

1 See Table 7.1 for key to abbreviations
2 Initial change in connectance is due to the entry of the new production units.

7.6.2 Secondary node loss

The network did not fragment under any of the interventions. Secondary node loss occurred in all but two interventions. The smaller aquaculture interventions, losing less mangrove habitat and so causing fewer primary removals, are the only interventions that do not lose nodes secondarily. Production units and trophic species are lost secondarily during the removal of vulnerability categories 7 and 6.

Secondary loss of species does not trigger a cascade of further losses. Secondary loss of production units does. The cascade begins with artisanal fishing (bay), and is followed by the loss of nodes that transact its catch. These nodes are poorly-connected, being part of a chain rather than a web of interactions. The cascade is caused by the removal of all species which the fishermen take, most of which are in vulnerability category 8. The lost production units will not necessarily become 'extinct', only disconnected from the Pagbilao network. The markets and their buyers will continue to buy catch from other of fishing communities. Of more importance is what happens to the local fishing community. In theory, other habitats in the bay will support the species on which they depend. If commercial and edible species do not become extinct throughout the bay, the worst impact on artisanal fishing is that fishermen might need to search further afield.

Even so, the demise of artisanal fishing is very likely. Artisanal fishing is currently a marginal activity. Fishermen are very poor. Children who have moved to Manila to find work supplement their incomes (Padilla 1996, pers. comm.). Fishermen are likely to be catching as much as they can in their attempt to make ends meet. In the absence of constraints on catch or effort, stocks are probably overfished and will come under further pressure with mangrove loss. Interventions that remove half or more of the mangroves cause local stock crashes that will force fishermen to extend their efforts further afield. They will face additional effort and costs. Loss of mangrove habitat is likely to drive a positive feedback exacerbating poverty and placing bay stocks under even greater pressure.

7.6.3 Change to connectance

Chapter 5 argued that change to connectance indicates declining network robustness. Table 7.6 shows that the effect on connectance from the entry of new production units is a very small decrease. The literature was used in Chapter 5 to infer that such a negative change to connectance from node addition could correspond to a very slight reduction in robustness. The main changes to connectance come from removing species. Figure 7.19 plots changes in standardised connectance against percentage of nodes lost for all interventions. Two interventions are shown per graph: forestry (subsistence and commercial); aquaculture 1 (semi-intensive and intensive aquaculture removing only 35% of the mangroves); aquaculture 2 (semi-intensive and intensive aquaculture removing 65% of the mangroves); and the combined forestry and aquaculture interventions.

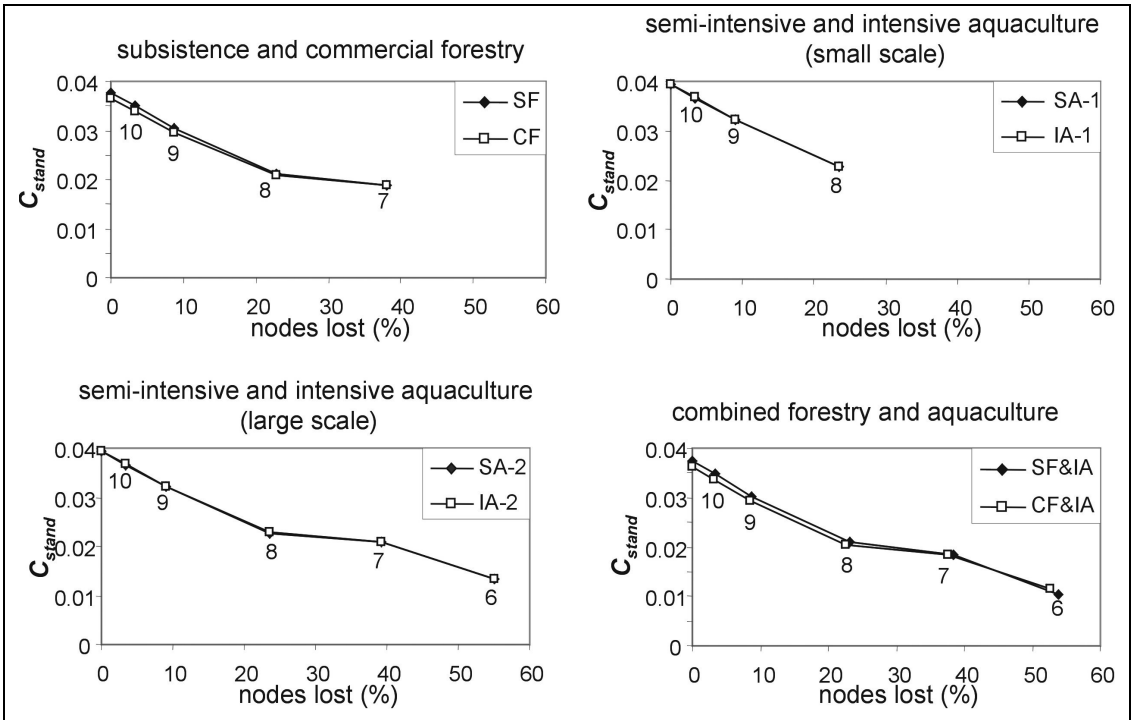


Figure 7.19 Change in connectance with intervention into the Pagbilao mangroves

The numbered coordinates indicate the change in connectance from removing a vulnerability category. Straight lines join the coordinates whereas the actual trajectory depends on the order in which species removed. In general, the figure shows that the more species

removed, the greater the change to connectance. The trajectories follow the same basic pattern, which begins with a steep decline in connectance with the removal of categories 10, 9 and 8. That this adversely affects network robustness is indicated by secondary loss of six nodes with the removal of category 7. The gentler slope with the removal of category 7 can be attributed to these secondary losses, which are poorly-connected. Further species removals trigger only two more secondary losses.

The figure suggests that network robustness has been substantially reduced in all interventions. Even though small-scale aquaculture causes no secondary losses, it takes only a few more species removals for secondary losses to occur.

7.6.4 Ranking the interventions

Interventions and the current situation are ranked according to their effect on the robustness of the socio-natural network. This effect has been measured by three indicators, but condensed to two because the network did not fragment. The criterion of secondary node loss leads to the following ranking of all interventions:

PR = SA-1 = IA-1 > SF = CF > SA-2 = IA-2 = SF/IA = CF/IA

where > denotes 'is better than' and '=' indicates 'is the same as'.

From the perspective of connectance change, the ranking is:

PR > SA-1 = IA-2 > SF = CF > SA-2 = IA-2 > SF/IA = CF/IA.

Multi-criteria analysis via the DEFINITE programme (Janssen & Herwijnen, 2006) has been used to generate an overall score and ranking, shown in Figure 7.20. Weights were assigned to the two indicators according to the weighted summation method.

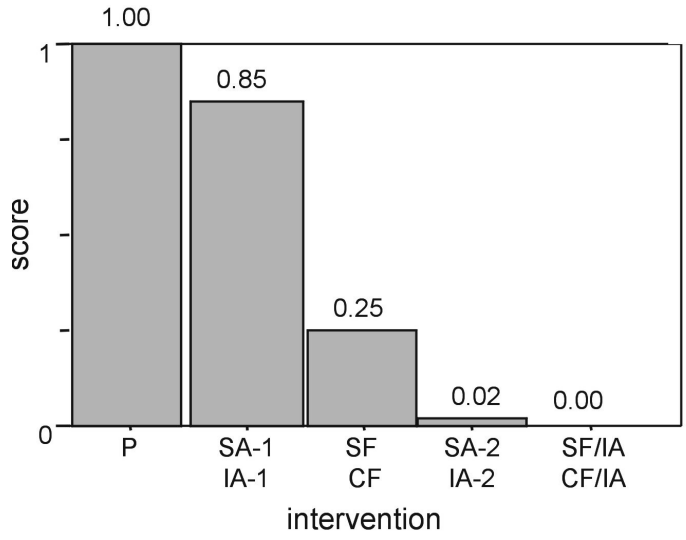


Figure 7.20 Score and ranking using multi-criteria analysis

The final ranking is:

PR > SA-1 = IA-2 > SF = CF > SA-1 = IA-1 >SF/IA = CF/IA.

Quite clearly, Preservation dominates all interventions because its socio-natural network does not change. Small-scale aquaculture, SA-1 and IA-1, dominate all other interventions. These two interventions do not cause secondary losses and lead to a smaller

change to connectance. The forestry interventions dominate the large-scale aquaculture and combined interventions. The ranking reflects the area of mangrove lost in the various interventions. Implications for management are discussed in Section 7.7.

It should be noted that the time over which these changes are effected to the current network is not specified and does not affect the ranking. For aquaculture, habitat loss would be more or less immediate, and species loss would probably occur in the short term. For the forestry interventions, habitat loss occurs over 30 years, and so species loss occurs more in long term.

7.6.5 Sensitivity analysis

Three sensitivity analyses were conducted, testing my assumptions regarding the habitat lost from forestry operations, the viability of smaller stands of mangrove, and uncertainty in the scores in Table 7.6.

My estimate of habitat loss from forestry is probably excessive. It is based on clear-felling practices, whereas forestry was originally designed to use selective logging and to have a lesser adverse effect on mangrove habitat. As has been stated, access, storage sites, etc. to facilitate selective logging may have disproportionately large impacts on habitat because the stand is relatively small. A spatial plan is needed to identify where boles are to be cut and how access routes and stockpiles could be located, and so to estimate habitat loss. The forestry interventions will perform as well as the small-scale aquaculture interventions if they cause only about 35% of habitat to be lost. To perform better, they would need to impact only 12% of mangrove habitat, and so prevent the removal of vulnerability category 8. All interventions based on forestry assume the effective prevention of poaching. This assumption is questionable. Even subsistence forestry would not meet local wood demand. Consequently, I would argue that the loss of 12% of habitat is excessively optimistic.

All interventions were designed to retain enough mangroves so that environmental services, notably, processing of pond wastes, sediment stabilisation and flood mitigation, would not be compromised. The various mangrove trophic species were placed in vulnerability categories 2, 3 and 4 in response to these assumptions. What happens to the network if these assumptions are unfounded – if the area and/or quality of the mangrove stand remaining after intervention is not sufficient for continued mangrove viability?

I have examined this question by removing all mangrove nodes (i.e. mangrove roots, mangrove seeds and seedlings, plants, live leaves, live wood, sap, pollen, nectar, fruit and flowers) from the reference network and from the final networks of the smaller aquaculture and forestry interventions. The loss of these ten mangrove nodes triggers cascading secondary losses in all cases. The number and order in which nodes are lost are not always the same, but it is essentially the same trophic species that are involved. Of concern are the production units lost secondarily. Forestry, wood collecting, and aquaculture, both new and existing nodes, are lost as a result of the removal of live wood and the secondary loss of dead wood, on which they all depend. My network analysis suggests severe economic and social impacts from failure of the mangroves.

The DEFINITE programme, used to generate the ranking of interventions, incorporates a Monte Carlo method to test uncertainty in scores. Figure 7.21 shows the results, testing

100% uncertainty of the scores per intervention and per indicator, shown in Table 7.6. The figure shows that the ranking is very stable to score uncertainty. Preservation usually occupies the first position, sometimes occupies second position, and only very rarely occupies any other position. Small scale aquaculture usually occupies the second position, sometimes the first position, and almost never any other position. Forestry occupies third position, rarely the second position, and almost never any other position. Large-scale aquaculture and the aquaculture/forestry mixes occupy fourth and fifth positions.

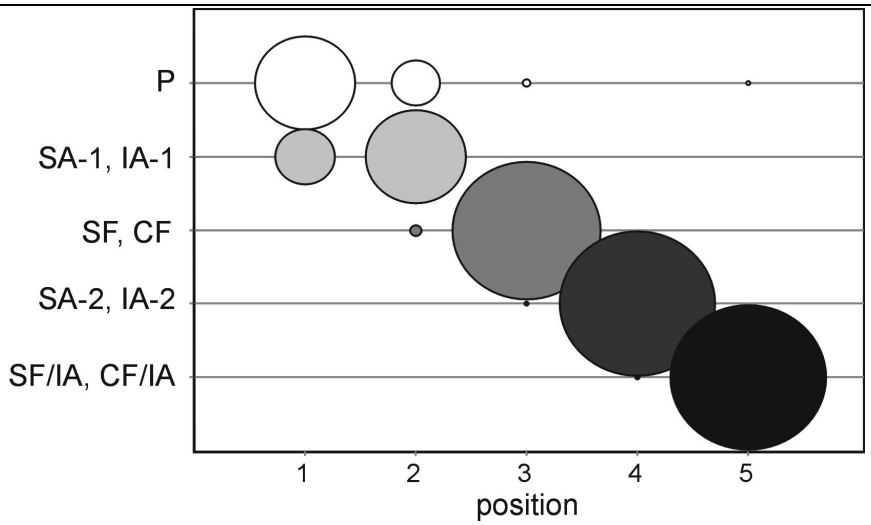


Figure 7.21 Sensitivity analysis of uncertainty in scores shows the stability of the ranking

7.7 Management implications

My analysis points to substantial risks from the conversion of the mangroves to aquaculture and forestry uses. Loss of mangrove habitat threatens the robustness of the Pagbilao socio-natural network, and specifically the viability of artisanal fishing lifestyle. My analysis shows that there is a threshold in habitat loss, somewhere between 35% and 50% loss, after which secondary nodes are lost. It also shows that network robustness was severely affected by habitat loss prior to this threshold. Even if the habitat threshold is not exceeded, the network is vulnerable to other sources of impact.

My ranking of interventions is almost the opposite of that from the earlier study (Gilbert and Janssen 1998):

SA-2 > IA-2 > CF/IA > SF/IA > CF > SF > PR.

Changes to this ranking occurred only under the most pessimistic scenario for failure of the sustainability conditions. Current management based on Preservation was deemed least desirable. Similar failure of sustainability conditions in my analysis only reinforces preference for Preservation. While there is conflict between the two analyses, the growing knowledge about this system makes it possible to identify promising compromises.

Gilbert and Janssen quite clearly show that there is much financial gain to be made from converting the mangroves. In the light of local poverty, the potential for such gains cannot be ignored. I identify two compromises, both of which have the potential of minimising adverse impact on network robustness while still yielding value. Each is discussed below. In both cases, management would aim to lose no more than 30% of the current

mangrove habitat. While adversely affecting the robustness of the socio-natural network, such management aims to fall short of the threshold for secondary node loss.

The first permits forestry operations. An advantage of forestry is that its 30-year rotation scheme means that habitat loss is gradual. This provides opportunity to monitor habitat loss and its effects on species diversity. In theory, operations could be curtailed if impacts were more severe than expected. Forestry could be established under a system of adaptive management (Walters 1997; Mee 2004), with a set of operational, short-term objectives paired with monitoring to support a long-term objective coined in terms of the robustness of the local socio-natural network and/or sustainable development of the study area. A foreseeable difficulty with forestry development is poaching. The subsistence forestry intervention generates wood products for local use but is not expected to meet local demand. Poaching is likely to continue, will continue to be difficult to prevent, and will compromise objectives targeting sustainable harvesting.

The second develops small-scale aquaculture, somewhat smaller than that assessed above. Assuming a linear relationship between value and size of fishponds, such an intervention could generate approximately US$350,000/year (semi-intensive aquaculture) or US$250,000/year (intensive aquaculture). Due to economies of scale, the actual figure is probably smaller, but would still be larger than the forestry options discussed above (approximately US$20,000/year). The main disadvantage with aquaculture options is that they involve abrupt and complete removal of mangrove habitat. There is no opportunity for a more adaptive management style as with the forestry options.

Janssen and Padilla (1999) used multi-criteria analysis (MCA) to make the trade-off between monetary and environmental values more explicit, as well as taking into account who derived benefit from mangrove conversion. While aquaculture generates, by far, the most value, this value accrues to wealthy individuals who neither live in the municipality nor employ local residents to manage the ponds. Conversion to aquaculture generates no local benefits; if anything it generates local costs due to the reduced income to artisanal fishing (see Table 7.2). As my analysis shows, it also increases the risk that this activity will be lost entirely.

The ranking of interventions derived from MCA is heavily dependent on the objectives of managers, and so on the weights assigned to the different criteria used to compare the performance of interventions. Janssen and Padilla showed that, with the large degree of conflict between environmental and economic values, and between equity and economic values, the ultimate choice of managers depended on who was making the decision. Table 7.7 repeats the set of decision makers considered by Janssen and Padilla, with their objectives and likely management preference.

The preferences of the fishpond owner and the sustainable world planner are unlikely to change as a result of my analysis. Changes are possible with the other three decision makers. My criterion for comparing interventions reflects the robustness of the Pagbilao socio-natural network. It has direct implications for sustainable development, which is the overarching goal of the sustainable planner. This decision maker might consider interventions into the mangroves that balanced monetary gains with a minimal loss of robustness. An adaptive management approach would appeal to this decision-maker, and so I would expect a preference for forestry.

Table 7.7 Decision makers, their objectives and their preferred intervention (Janssen & Padilla 1999)

Decision maker	Objective	Management preference
Fishpond owner	Maximise profit	Semi-intensive aquaculture
Local government	Maximise net income to local government and to the local population	Convert to fishponds, increase licence fees OR Forestry
Social planner	Maximise total benefits AND More equal income distribution	Conversion to fishponds OR Forestry
Sustainable planner	Maximise total benefits AND More equal income distribution AND Maintain minimum level of environmental stocks	Preservation
Sustainable world planner (e.g. UNEP/GEF)	Maximise global environmental benefits from mangrove forests	Preservation, and compensate for loss of income OR Accept loss of the Pagbilao forest

In its specification of interactions among actors in the study area, my analysis provides a detailed and explicit way for local managers to consider sustainable development while supplementing insights into the welfare of local communities. Local government might also prefer forestry, and particularly subsistence forestry, which directly addresses local needs, but might also be swayed by the income to be gained from fishponds. License fees with the conversion to aquaculture could be used to compensate local communities and to stimulate the local economy.

The social planner, in Janssen and Padilla's assessment, was already choosing between forestry and aquaculture. My analysis could lead to the social planner's acceptance of smaller-scale aquaculture (which the fishpond owner probably would not accept) due to concern about the potential loss of traditional lifestyles – namely artisanal fishing. The choice between aquaculture and fishing remains directly linked to this decision-maker's emphasis on economic gain (therefore aquaculture) versus income distribution (therefore forestry).

7.8 Conclusions

This chapter reanalysed earlier research into the management of a mangrove stand in the Philippines. The new analysis directly addresses issues that were relevant to the decision problem, but could not be incorporated in the earlier approach. It is the relatively recent emphasis on coevolution and techniques for assessing networks robustness that have facilitated this reanalysis.

I identified four constraints to Gilbert and Janssen's analysis at the beginning of the chapter. Their design of interventions emphasised sustained mangrove, rather than sustained ecosystem, viability. Ecosystem sustainability is likely to be adversely affected given that human intervention involves the loss of mangrove habitat and species. Gilbert and Janssen did not address the potential for irreversible biodiversity loss, largely because it is difficult to place values on irreversible losses in the approach. My analysis deals explicitly with biodiversity and its loss. Thirdly, Gilbert and Janssen acknowledged that the approach did not take into account the potential for regime shifts. Uncertainty and unpredictability were seen to be functions of the high degree of interconnectedness within the mangrove ecosystem and between it and its users. By focusing on interactions, I have addressed interconnectedness explicitly. The likelihood of a regime shift is indicated by fragmentation of the network of interactions, and secondary loss of nodes. Finally, the earlier approach focused on valuation, and so is driven by economic considerations. Environmental services were valued only indirectly. Consequently, there is an intrinsic mismatch between economic and environmental information. By emphasising interactions, topological network analysis treats environmental and economic actors equally. It is truly integrated.

The new approach also has constraints. While my focus on interaction permits integration of economic and environmental aspects, I am not able to weigh the interactions or consider substitution among interactions. Competitive interactions among nodes are also ignored.

My approach constructs a socio-natural network mapping interactions among the various entities associated with the Pagbilao mangroves. Human intervention means the addition of new production units to the network, with the entry of new mangrove users, and the loss of species due to loss of mangrove habitat. The addition of production units is relatively straightforward. Estimation of the loss of species, both number and order, was based on current knowledge.

The small-scale aquaculture interventions, included in my analysis but not treated by Gilbert and Janssen, convert less mangrove. These interventions perform as well as Preservation in that no nodes are lost secondarily. However, changes to connectance suggest that network robustness is adversely affected. The forestry interventions lose nodes secondarily. However my estimate of habitat loss could be excessive; it is quite feasible that they would perform as well as small-scale aquaculture. Habitat and species are lost over the rotation period with forestry. This means that there is potential for applying adaptive management principles, monitoring habitat and species loss, and reducing wood extraction if impact is excessive. An additional attraction of the forestry interventions, implemented in the context of adaptive management, is that they would provide the opportunity to monitor species and habitat loss, and to contribute to our knowledge regarding species' response to habitat loss.

If any alternative to current management were to be considered, the small-scale aquaculture and forestry interventions show that performance can be linked directly to the amount of mangrove habitat lost. The aquaculture interventions that performed well in value terms, perform poorly in terms of their impact on the socio-natural network because they result in the loss of much habitat. The combined aquaculture and forestry interventions perform no better since they affect the same area of habitat. The current

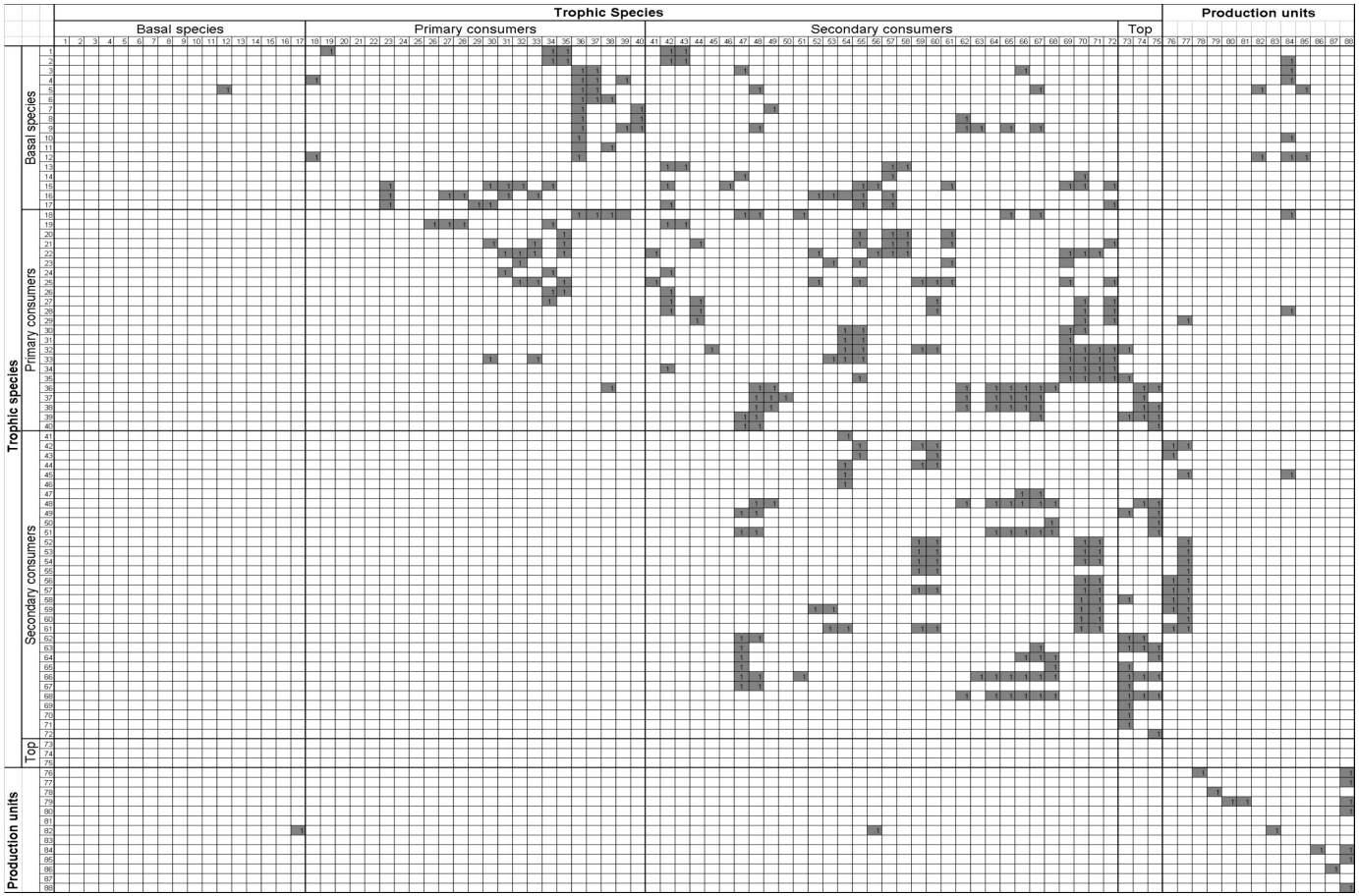
situation, Preservation, performs best because it causes no loss of habitat. The small-scale aquaculture and the forestry interventions are intermediate in performance. While aquaculture performs better than forestry, there are uncertainties regarding how much loss of habitat forestry would generate. There is a distinct possibility that it would be less habitat than what I have estimated.

The potential for generating greater value from the mangroves under different management is difficult to ignore given poverty in the study area. Consequently, the forestry and small-scale aquaculture interventions require further consideration. Loss of 35% of the mangrove, while not triggering secondary node loss, still has a substantial impact on network robustness. The forestry interventions offer the advantage of implementing adaptive management strategies. The impact of forestry on mangrove habitat can be monitored, and forestry practices adjusted, as needed, should habitat loss exceed this maximum or should species loss be greater than estimated.

Such a management structure is not possible for aquaculture, which will involve the abrupt loss of habitat with pond construction. On the other hand, this intervention is likely to generate significantly greater revenues. While little benefit from fishponds currently accrues to the local human population, a system of license fees could be implemented to distribute benefits more equitably. The choice between forestry and aquaculture remains a difficult one.

Finally, I argue that my approach would encourage concordance between national and local managers. Janssen and Padilla's (1999) assessment of the different decision makers and their objectives suggested very different preferences among them.

Appendix I. The socio-natural network for the Pagbilao mangroves (darkened cells indicate interaction or a cell entry of '1'; unfilled cells indicate no interaction or a cell entry of '0')



Appendix II. The nodes of the socio-natural network

ID	Name
1	mangrove roots
2	mangrove seeds and seedlings
3	plants
4	live leaves
5	live wood (including *Nipa* shingles)
6	sap
7	pollen
8	nectar
9	fruit
10	flowers
11	lichens
12	dead wood
13	micro-epiphytes (algae)
14	macro-epiphytes
15	benthic algae
16	phytoplankton
17	detritus
18	fungi
19	benthic bacteria and fungi
20	microfauna
21	meiofauna
22	microprotozoa
23	zooplankton
24	epiphyte-grazing amphipods
25	isopods
26	suspension-feeding molluscs
27	small filter feeders on hard surfaces
28	large filter feeders on hard surfaces
29	epiphyte-grazing gastropods
30	deposit-feeding polychaetes
31	suspension-feeding polychaetes
32	herbivorous shrimp
33	deposit-feeding peracaridan crustaceans
34	hermit crabs
35	spider crabs (herbivores)
36	insects on flowers and fruit
37	insects on leaves
38	other herbivorous insects
39	fruit-eating birds
40	fruit-eating bats
41	predatory shrimps
42	omnivorous crabs
43	mud crabs
44	predatory gastropods
45	other gastropods
46	predatory polychaetes
47	(ecto)parasites
48	insectivorous insects
49	insectivorous bats
50	spiders
51	other arthropods
52	fish feeding on epifauna
53	ovivorous and planktivorous fish
54	resident carnivorous fish
55	resident gobies
56	milkfish (transient)
57	herbivorous fish
58	mullet (transient)
59	transient piscivorous fish
60	resident piscivorous fish
61	transient shrimp (penaeids)
62	insectivorous birds (1)
63	rat
64	small lizards
65	insectivorous birds (2)
66	large lizards
67	insectivorous birds (3)
68	big arthropods
69	benthos-eating birds
70	fish and crustacean-eating birds
71	fish-eating birds
72	gulls
73	raptors
74	owls
75	snakes
76	artisanal fishing (bay)
77	artisanal fishing (mangrove)
78	buying for Pagbilao markets
79	Pagbilao markets
80	local hotels and restaurants
81	buying for Manila market
82	extensive aquaculture
83	buying of aquaculture product
84	collecting of minor mangrove products
85	wood collecting
86	mangrove nursery
87	afforestation programs
88	local community

8. Conclusions and Recommendations

"……it is turtles all the way down."

e.g. Geertz, 1973[1]

8.1 Introduction

Natural and social systems interact. Components of each system interact among themselves and with components of the other system. Interaction provides the basis for coevolution, with system components, the nature, strength and pattern of interaction, system processes and emergent system features changing over time. The goal of my dissertation was to develop the means for comparing different human interventions into ecosystems with regards to their impact on the future coevolution of interacting natural and social systems. My specific research objectives were to develop the two elements comprising such means: a method that simulates the impact of intervention on coevolution, and a criterion and associated indicators for comparing different interventions.

The method, termed topological network analysis, assesses generalised coevolution. It involves the construction of a socio-natural network, translating different human interventions into changes in the network, and comparing the impact of such changes on the network's robustness. Robustness is the criterion developed in this dissertation. It is measured in terms of three indicators: fragmentation, secondary node loss and change in connectance. The relevance of these products for future coevolution lies in three points.

Firstly, the baseline conditions for future coevolution are estimated by the method. Topological network analysis captures the pattern of interactions among system components. Interaction is one factor driving each component's evolution. As argued by Kauffman (1993), individuals tend to adapt myopically, with small changes in local interactions because they cannot oversee the effect of adaptation on the adaptive landscape of the larger community. Human intervention in ecosystems effects changes in the pattern of interactions, and potentially at such a scale that this adaptive landscape is substantially distorted. The distortion is not measured. The specific path of future coevolution is not specified, which in any case would be a particularly brave undertaking. However the potential for such drastic change to cause the system shifts to a new state is indicated. A shift to a new system state implies new conditions driving coevolution.

Secondly, the method captures one crucial aspect of evolution. It focuses on species extinction, even if only locally, and so the inability of system components to adapt quickly enough to changing circumstances.

Finally, my method comprises the three elements identified by Winder *et al*. (2005) as requisite for an analysis of coevolution as opposed to co-dynamics. The socio-natural network comprises entities capable of continued existence and of being selected on the basis of fitness. It captures diversity within a socio-natural system; human intervention, by introducing new economic activities within an ecosystem, is one source of increased diversity. Increase in diversity leads to winnowing of overall diversity by the differential impact on components' extinction risk.

This chapter has the following objectives:

- to recapitulate on the dissertation's 'story line' and summarise the main steps taken and conclusions drawn;
- to evaluate the method's potential; and,
- to make recommendations for further research.

8.2 Recapitulation of the dissertation's findings

8.2.1 The dissertation's 'storyline'

Chapter 1 uses diagrams to illustrate various perspectives on interactions between natural and social systems. Subsequent chapters build on these diagrams to illustrate subject matter and focus per chapter. Placed side-by-side, the figures depict the dissertation's storyline. Figure 8.1 compares the beginning of my story from a view on coevolution from Chapter 1, with its end in Chapter 7. The two figures differ substantially. Figure 8.1a represents the perspective of Lorenzoni *et al*. (2000a) on coevolution. Interactions among system components and between the two systems drive system change. The sustainable development debate highlights concerns that social impact is effecting changes to ecosystems such that future interactions will seriously constrain the direction of social change. While this diagram does not distinguish between co-dynamics and coevolution, changes in the nature and strength of interaction between the two systems provide the template for future coevolution.

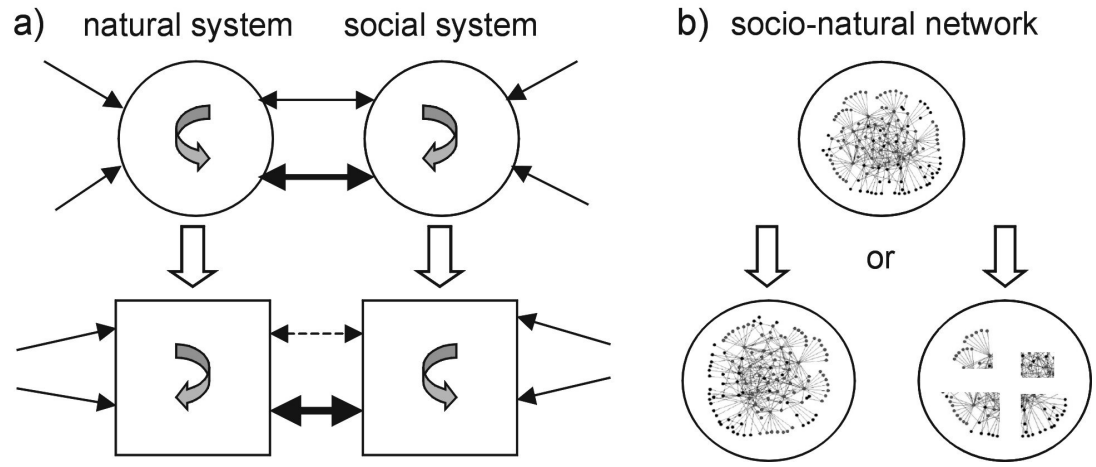


Figure 8.1 Perspectives on coevolution: (a) from Lorenzoni et al. *(2000a) at the beginning of this dissertation; (b) to my perspective in the case study in Chapter 7*

My dissertation leads to a different perspective on coevolution, as can be seen by comparing Figures 8.1a and b. There are three main differences. Firstly, I no longer distinguish between natural and social systems. I emphasise a socio-natural network, comprising interacting components of a social and a natural systems. In this I follow McGlade (1995, in Leeuw & Aschan-Leygonie 2000) who argued that there is neither a social system nor a natural system, only socio-natural interaction. Redman *et al*. (2004) also advocate abolishing the distinction between social and natural systems, and their treatment as a single, complex system. Secondly, Figure 8.1a's unspecified change within the natural system is specified in Figure 8.1b, which identifies extremes in coevolution. The system can remain essentially intact (on the left), or it can lose components and fragment. Thirdly, interactions among system components are specified and their pattern is highlighted in Figure 8.1b.

The first half of my dissertation reviews the literature and identifies elements for generalising and operationalising 'coevolution' to support environmental management. It reviews the literature on evolutionary and coevolutionary concepts as they might apply to our understanding of interaction between social and natural systems. The process of mutual change, whereby each participant in an interaction causes and responds to changes in the other, is termed coevolution. I place emphasis on natural systems, specifically ecosystems. This is due, in part, to my expertise. However ecosystems are one natural system experiencing adverse impact from social systems, and these impacts are potentially capable of rebounding on at least some social system components.

The literature review yields three main products that are carried into the second half of the dissertation where the method and criterion are developed and tested. The first is a categorisation of social impact on natural systems and the interactions that cause them. Conventional images of interaction between social and natural systems emphasise the extraction of environmental goods and services, and the release of substances and organisms, by social systems. Two categories of social impact – social predation and habitat loss and fragmentation – pertain to the former. Emissions and biotic exchange pertain to the latter. The hallmark of social impact is the loss of species and so of biodiversity. Biodiversity appears to convey stability to ecosystems, although specifics of the relation-

ship are still subject to debate. My method specifically addresses biodiversity loss and its effect on robustness, one of a range of stability concepts.

The second is the adaptive cycle, which describes the progress of systems through phases of growth and conservation, followed inevitably by release and reorganisation; reorganisation may see the emergence of a new system state or regime. Movement through the growth and conservation phases coincides with coevolution of systems components, as different mixes of components and interactions are tested for their ability to 'fit' together. As highlighted by Garcia (1999), evolutionary change by a system component can trigger readjustment of other interlinked components and lead simply to changes in the phenotypic mix comprising the system. It may also lead to a cascade of effects and the system's 'destruction'. These extremes in system outcome are captured in Figure 8.1b. I focus on extinction as one form of evolutionary change, and the transition from conservation to release as a system's connectedness breaks down.

The third is a focus on network topology and on measures of network robustness. Networks map interactions among system components. Recent research into their robustness with node loss shows that the response varies with the network's topological features and with the type of node lost. Food webs are one form of 'real world' network that have been subject to such analysis, but the protocols for species removal have been based more on network characteristics (connectedness) than on perceived risk of extinction. Social impact is one factor driving this risk.

These three products from the literature review provide the basics for developing a method for assessing the generalised coevolution of socio-natural networks. The second half of the dissertation develops the method and criterion in three steps. The first step introduces the basics of the method (removing species from networks), develops connectance as a measure of network topology, and examines its capacity to reflect changes in network robustness. The second step develops protocols for species loss by identifying species at risk from the various sources of social impact. These protocols are tested on two food webs. The third step examines ways in which social and natural networks could be linked or combined so that reciprocal effects of species loss on both systems can be traced. The method is demonstrated for a stand of mangroves in the Philippines.

8.2.2 Milestones in the 'storyline'

Chapter 1 identified steps in my research approach. These have led to the following milestones marking progress from Figure 8.1a to Figure 8.1b:

1. identification of four broad types of social impact visited on ecosystems by social systems, as well as their ecological and evolutionary consequences (Chapter 2);
2. analysis of the range of interactions and (co)evolutionary responses between species, drawing lessons for environmental management (Chapter 3);
3. coevolution among the components of complex adaptive systems, leading to a focus on the adaptive cycle, networks and recent research into network topology and robustness (Chapter 4);
4. assessment of connectance, a measure of network topology, and its capacity to indicate changes to network robustness (Chapter 5); and,

5. the incorporation of the social system by developing realistic protocols for species loss and combining components of both social and natural systems in a socio-natural network (Chapter 6).
6. the illustration of topological network analysis and robustness as evaluation criterion for comparing alternative interventions into a mangrove stand in the Philippines.

The first milestone identified four types of social impact: social predation, emissions, habitat loss and fragmentation and biotic exchange. Their ecological effects lead to biodiversity loss, which has become the hallmark of global social impact. A more evolutionary perspective highlights the possibility that we are entering another mass extinction event. In past mass extinction events, species apparently well adapted to their environment were lost, possibly indicating the fragmentation of ecological networks and cascading secondary extinction. Because centuries, if not millennia, were needed for ecosystem reconstruction, a current mass extinction event raises concerns that social impact may be causing very long-term constraints to human development.

The second milestone provides a salutary reminder, not only that there are many types of interactions, but also that there are may be different evolutionary responses to them. Some species remain in a spiral of antagonism, whereby defensive adaptations lead to counter adaptations, lead to defensive adaptations, and so on. This form of evolutionary response is clearly occurring in disease and pest management. That it might be occurring in many socio-natural interactions is cause for concern. Other evolutionary trajectories were identified, by which species derive by-product benefits that reduce the cost of interaction. Topological network analysis does not allow for evolutionary change in the nature of interaction. Since such change occurs in nature, it is reasonable to expect it to occur in socio-natural interactions. However widespread species extinction is evidence that species are unable to adapt to social impact.

The third milestone derives from a review of a very complex subject. There are various perspectives on coevolution within the study of complex systems. The adaptive cycle has become a key conceptual approach for examining the evolution of ecological systems as well as interacting ecological and social systems. My focus on networks derives from two factors. The first is that specification of actors and interactions is integral to any understanding of the coevolution of natural and social systems. The construction of a network, whether in the form of nodes and links, a matrix, or some other form, requires such specification. Figure 8.1a might illustrate coevolution, but it provides no detail on who is interacting with what and whether the interaction persists over time. The second factor is recent research into the topology and robustness of ecological networks, specifically food webs. Food web research has a long history within ecology. By examining the robustness of food webs to species loss, Dunne *et al*. (2002a and b) have built a bridge linking ecological theory with the study of complex networks and complex systems.

The fourth milestone expands on research in Dunne *et al*. (2000b). These authors compare responses to species loss across food webs with differences in connectance, whereas I investigate the impact on connectance of species loss from food webs. They compared different food webs in terms of their robustness, whereas I assess how adversely robustness is impacted by species loss. I conclude that any change to connectance indicates declining network robustness; with species loss, sharp, negative changes in particular indicate adverse impact on robustness. I hypothesise that, if possible changes to connectance

can be estimated, human interventions into ecosystems could be compared in terms of their likely impact on network robustness and ultimately on system stability.

The fifth milestone is two-sided, addressing steps to be taken before my hypothesis can be tested. Firstly, it develops more realistic protocols for species removal. There is no *a priori* reason why connectedness, the criterion for species removal used by Dunne *et al*. (2000b), should correlate with actual extinction risk. I return to the four categories of social impact in Chapter 2, identify the ecological characters of species most vulnerable to extinction and then translate these characteristics into possible network characteristics. The effects of these more realistic protocols are tested on two food webs.

Development of more realistic protocols for species loss means expansion of the analysis to include the social system, but in one direction only – the effect of social systems on species. The second side of this milestone examines how social and natural systems can be integrated into a single, socio-natural network so that reciprocal effects can be traced. In theory, networks could be constructed to map a range of different types of interactions. I narrow down the type of interaction to consumption, with both biological and economic meanings so that matter and energy flow from one system component to another. A binary criterion – presence or absence of interaction – drives network construction in the form of a predation matrix. The dynamic nature of interactions, as illustrated in Chapter 3, or the capacity of nodes to change their consumption preferences, is ignored. The approach is static, but it still provides insights for future dynamics.

8.2.3 Method and criterion applied

The sixth milestone applies both the method and the evaluation criterion. Topological network analysis comprises four steps: construction of a socio-natural network for an ecosystem and associated human activities; specification of different human interventions into this socio-natural network; translation of these interventions into the addition and/or loss of nodes from the network; and, comparison of alternatives in terms of their estimated impacts on network robustness. The comparison of interventions according to their impact on the robustness of the socio-natural network leads to management insights. The method is illustrated for changes in the management regime of a mangrove ecosystem on which the local community is dependent.

The type of social impact

Chapter 2 groups social impact into four broad categories. Chapter 6 identifies topological network analysis as having potential to provide management insights for issues dealing with social predation and habitat loss and fragmentation. While the economic part of the Pagbilao socio-natural network documents social predation, the management issue is one of habitat loss. Habitat loss occurs with the entry of new mangrove users – notably forestry and aquaculture – into the local economy. Forestry removes individual mangrove trees while aquaculture clears whole areas of mangrove and replaces them with fishponds. The eight alternative interventions into the mangroves are based on an earlier study of the Pagbilao mangroves. Two types of forestry, two types of aquaculture, as well as forestry-aquaculture combinations are considered.

While the management issue revolves around habitat loss, current social predation is likely to be placing at least some species at risk of local extinction. Artisanal fishermen can be expected to be catching as much as they can, with the only constraint on catch being the use of traditional rather than modern fishing methods. Species targeted by fishermen are not the most vulnerable to habitat loss, but my assessment of species vulnerability still places them at considerable risk. It is their removal that triggers secondary loss of artisanal fishing and associated production units in a number of the management alternatives. The difference between the small-scale aquaculture and the forestry alternatives lies with these secondary losses. The aquaculture alternatives lose no nodes secondarily, yet all fished species except two species of crustacea have been lost. The actual viability of artisanal fishing in such a situation must be considered highly unlikely.

Methodological issues for network construction

Construction of the predation matrix for the mangroves is heavily based on the literature, augmented by species lists for the mangroves. Construction of the economic matrix focuses on extraction of mangrove species and their subsequent transactions through the local economy. Three methodological issues for the construction of socio-natural networks were identified in Chapter 6.

The first is resolution. Specification of trophic species and production units attempted to match resolutions of the two component matrices. Species in the predation matrix represent trophic species, a function rather than taxonomic concept that is defined in terms of common prey and predators. Production units in the economic matrix are distinguished on the basis of similar production processes and so on similar inputs and outputs. In terms of a predation matrix, trophic species and production units are distinguished on the basis of taking matter from similar rows and delivery matter to similar columns.

The second is the type of interaction. Only interactions involving the flow of matter and energy, originating from the mangrove ecosystem, are documented. Other goods transacted by the local economy – home produce as well as purchased items – are not included. The inclusion of such transactions would not change my analysis, as these transactions are not influenced by loss of mangrove habitat.

The third is spatial extent. My analysis focuses on an ecosystem and its immediate users, and so its spatial extent is tightly bounded. Species interactions that do not occur in the mangroves, such as the consumption of fish by sharks in Tayabas Bay, even though the fish may have matured in the Pagbilao mangroves, are not documented. Economic transactions outside the municipality of Pagbilao, such as the sale of prawns at the Manila fish markets, are not documented. The spatial extent of my analysis matches the spatial extent of the decision problem –use of the Pagbilao mangroves. A different spatial extent would be needed for other decision problems, such as whether to allow commercial fishing trawlers to operate in Pagbilao Bay. The focus on commercial species and on the bay as a whole would lead to inclusion of more bay ecosystems. Issues of habitat fragmentation, with loss of mangroves, coral and seagrass and their interconnections, as well as the continued viability of artisanal fishing, could be examined using topological network analysis, but require a different spatial extent.

Uncertainties in specifying node loss

Translation of the management alternatives into changes to the network requires specification of new production units and links added to the network, and of species lost from the network. The former is relatively straightforward. It is worth noting that the entry of new production units tends to add a 'chain' of interactions to the network, rather than a 'web', and has only a small impact on connectance. Specification of the species lost is not straightforward, and introduces elements of uncertainty.

The area of habitat lost due to the new economic activities must first be estimated. For forestry, this area is estimated on the basis of clear-felling practices and so is likely to be an overestimate. The degree of overestimation is uncertain. The potential damage from ancillary forestry activities (access routes, stockpiles, etc.) could well be disproportionately large in such a small stand, and my overestimate an underestimate. A spatial plan for selective logging is needed to assess forestry's impact on habitat more accurately.

Habitat loss is used to estimate the number of species that will be lost. While based on available literature, this estimate is clearly uncertain. Current knowledge of the relationship between habitat and species loss is limited, with most efforts to date focusing on large areas of terrestrial habitat. While a linear relationship looks likely, discontinuities, truncation etc. are all possible, particularly when only a small amount of habitat, such as the Pagbilao mangroves, remains. Even so, I would argue that the linear relationship used in Chapter 7 is a reasonable approximation.

To identify the particular species lost, I classified species from the predation matrix in terms of their vulnerability to habitat loss, and then removed them sequentially. My classification draws from the literature, but there is still much to be learned here. Most particularly, the literature focuses on (terrestrial) mammal and bird species. Crucial species in my case study are aquatic, notably fish and crustacea, and are transient in the mangrove ecosystem, being present only as juveniles.

Indicators of declining robustness

My dissertation identifies three indicators of declining robustness, and equates declining robustness with increasing likelihood of a regime shift. Two indicators, secondary node loss and network fragmentation, derive from the definition of robustness. I identify a third: change in connectance. These three indicators provide the basis for comparing the performance of management alternatives. However, they cover different parts of a spectrum of adverse impact on robustness. The spectrum ranges from a fully operational, connected system where adverse impact is minimal, to unconnected system components, corresponding to the worst possible impact on robustness and dissolution of the network. This spectrum and the indicators are shown in Figure 8.2.

Change in connectance gives the earliest warning that robustness is declining. As shown in Chapter 5, any primary removal will cause a change in connectance, but it is the loss of well-connected nodes and sharp declines in connectance that give the strongest indication of adverse impacts on robustness. Such changes may be seen as harbingers of impending secondary node loss. Once secondary node loss occurs, the clarity of this indicator is lost. Secondary losses tend to involve poorly-connected nodes, and cause connectance to decline less sharply, or even increase. All alternatives to the current manage-

ment regime for the Pagbilao mangroves generate strong negative changes in connectance from the first primary removals, indicating that loss of mangrove habitat will adversely affect the robustness of the socio-natural network centred on it.

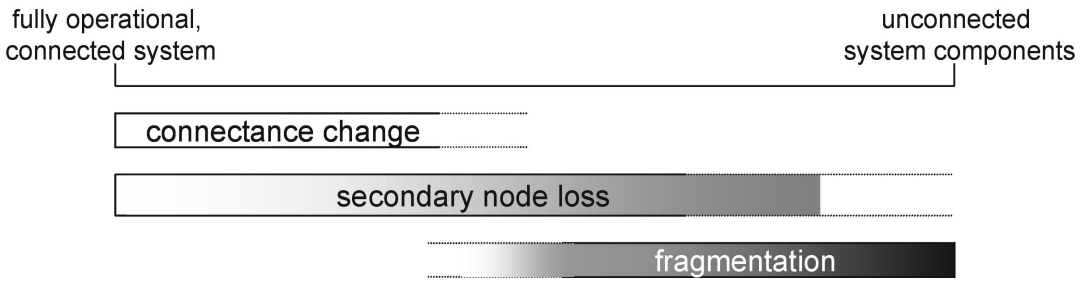


Figure 8.2 The three indicators of declining robustness form a sliding scale and provide different insights into the likelihood of a regime shift (the darker the shading, the greater the likelihood)

Secondary node loss can occur with the first primary removal; this occurred with the loss of a parasite on the most-connected species from the El Verde rainforest food web (see Chapter 5). More commonly, secondary node loss occurs after a number of primary removals and precedes network fragmentation. Cascading secondary loss can be a precursor of fragmentation, or indicates that fragmentation has occurred. For the Pagbilao network, such losses occur after more than 20% of species have been primarily removed, which equates with loss of half of the mangrove habitat.

Fragmentation indicates the greatest impact on robustness, by which the network breaks down into sub-networks and loses nodes secondarily. The Pagbilao network did not fragment under any of the management alternatives.

The likelihood of a regime shift is also indicated in Figure 8.2, generally increasing with declining robustness. The adaptive cycle (Chapter 4) argues that progress from the release to the reorganisation phases is associated with loss of connectedness. A loosely defined, largely unconnected, system can easily be reorganized by small inputs and shaped by chance events, making it difficult to predict what type of organization will form. A new system state may emerge. Robustness is defined in terms of secondary node loss and fragmentation, and is also indicated by change in connectance, particularly sharp declines in connectance. Consequently robustness is lost as connectedness is lost, and declining robustness may be paired with increasing likelihood of a system state change.

Fragmentation represents a substantial loss of connectedness among system components and so introduces the greatest potential for a regime shift. While small negative changes to connectance also indicate reduced connectedness, the likelihood of a regime shift must be very small, although dependent on the specific network and the nodes at risk of extinction. The figure shows that secondary node loss brings with it some potential for a regime shift. Corroboration for this can be found in the case study and from the literature. Research by a number of authors, such as Andrén (1994), With and Crist (1995) and Vermaat *et al*. (2004), suggests a threshold in system states at around 50-60% loss of habitat. Secondary node loss in my case study occurred around this proportion of habitat loss, and so could well be indicating an actual or imminent regime shift in the Pagbilao network. This explains the light colouring in Figure 8.2 with secondary node loss. Since

the clarity of change in connectance is compromised by secondary node loss, I consider that connectance change provides no insights into the likelihood of a regime shift.

8.3 Effectiveness of topological network analysis

Effectiveness is the degree to which desired objectives are achieved. The objectives of my dissertation were to develop two elements that would provide the means for comparing different human interventions into ecosystems with regards to their impact on future coevolution. The two elements comprise a method that simulates the impact of intervention on coevolution; and a criterion and associated indicators for comparing the impact of different interventions on a socio-natural network.

The effectiveness of this dissertation's products depends on three issues. The first relates to the relationship between declines in robustness and the likelihood of a regime shift. The second relates to construction of a socio-natural network and the simulation of human interventions by removing species from a network. The third relates to the types of environmental issues that can be sensibly addressed by topological network analysis.

The relationship between declining robustness and increasing likelihood of a regime shift derives from Holling's adaptive cycle, as discussed in Chapter 4. The adaptive cycle plots the course of a system as it slowly grows and consolidates in one metastable state or regime, then undergoes rapid transition that may result in a new one. Intrinsic to the adaptive cycle is that a breakdown in connectedness among system components coincides with this transition. Robustness is defined in terms of secondary node loss and network fragmentation, both of which constitute a breakdown in connectedness.

The logic behind the adaptive cycle and examples such as wildfires are appealing. The occurrence of episodes in some systems has long been recognised, for example boom and bust episodes in economies, or the rise and fall of civilisations. The adaptive cycle places episodic events in a slightly different context and serves to focus attention on events preceding and contributing to 'crashes' or regime shifts. Implicit in the adaptive cycle is that we might be able to manage systems to avoid shifts or minimise their adverse impacts. Proponents of the adaptive cycle argue for flexibility to be 'managed' into systems and for close monitoring of indicators of systems' dynamics (e.g. Carpenter 2002). Robustness could be seen as one in a suite of such indicators.

The indicators for robustness can be quantified but their values are relevant only with a particular decision problem. For example, a decline in connectance of 0.03 could have different implications for different networks or in different contexts. Alternative futures are compared with regards to these values, and the comparison provides decision-makers with insights as to the repercussions of their decision. Information regarding the likelihood of a regime shift is considered pertinent to many environmental decision problems.

The second issue relates to the construction of socio-economic networks and the simulation of human intervention by removing of species. As is shown in the case study, construction of a socio-economic network is not particularly difficult. There is a growing body of literature on feeding relationships in ecosystems, which should allow representation of a particular food web. The construction of the economic matrix and its linkage to the food web is also not difficult. A socio-natural network, constructed with care, should be a reasonable proxy of actual socio-natural interactions.

Human intervention into the ecosystem is simulated by removing species. Clearly topological network analysis is best applied to decision problems or management issues involving differential effects on species' survival. With biodiversity loss as the hallmark of social impact, there would seem to be abundant instances where topological network analysis can be applied. However there are two types of uncertainty inherent in this method. The first is that the correct number of vulnerable species can be specified. As was seen for the case study, there is still much to be learned here, and particularly with regards to impact of habitat loss and fragmentation on species.

The second uncertainty relates to how secondary losses are identified. My method, following Dunne *et al*. (2002b), incorporates an algorithm that loses species secondarily when its last prey, or last link to a food web, is lost. It is possible that secondary extinctions are overestimated since species can survive by switching to less preferred prey. The algorithm accounts for this effect only to the degree that less preferred trophic links are included in the original food web and thus delay the onset of a secondary extinction. It is also possible that the potential for cascading extinctions is underestimated, since species losses can result in strong non-trophic and indirect effects.

The third issue relates to the type of social impact that can be sensibly simulated by topological network analysis. Chapter 6 showed that the greatest potential for topological network analysis was associated with issues causing social predation and habitat loss and fragmentation. With the latter occurring at global scales, and the former now affecting multiple species in some ecosystems, there is again much opportunity for the application of topological network analysis.

Chapter 6 also showed that the effects of removing basal species yield results that are not easily interpreted. The loss of basal species clearly causes severe impacts on food webs, particularly when they are dependent on only a few such species. The loss of basal species through habitat loss and fragmentation raises non-trivial questions such as 'when is a forest no longer a forest'. Eutrophication changes basal species, but via indirect effects, namely shifts in competitive balances, rather than direct loss. Indirect effects cannot be captured by topological network analysis. Biotic exchange involves the addition of species to ecological communities. Such addition to food webs is, as yet, not well understood, either in general or from a topological perspective. Consequently the relevance of topological network analysis for such environmental issues is unclear.

Topological network analysis and robustness offer an effective way of comparing alternative human interventions into ecosystems, particularly where species losses and the possibility of a regime shift are involved. Defining efficiency as effectiveness divided by the cost (or effort) of achieving that level of effectiveness (e.g. Janssen 1992), my dissertation's products may also be categorised as efficient. The effort involved in constructing a socio-natural network and in translating alternatives into changes in nodes and links is not large, as demonstrated by the case study in Chapter 7.

8.4 Recommendations for further research

The discussion above and the bounds placed on this dissertation in Chapter 2 suggest a number of areas where further research is needed. I identify four high priority directions.

Species at risk of extinction

Application of topological network analysis requires specification of the species at risk of extinction from human interventions. This is not always straightforward, as was clear in the case study. There are two aspects of this issue that require further research.

Firstly, while there is considerable knowledge about the ecological effects of social impact, translation of species' ecological features into their topological features presents challenges. I made a number of assumptions in Chapter 6 regarding the connectedness of species as risk from social impact. For example, I assumed that species targeted by social predation are highly-connected. Assessment of the 'knock-on' effects of losing vulnerable species requires an understanding of the role of species within ecological networks.

The second aspect relates specifically to habitat loss. The relationship between habitat area and species loss clearly needs further effort. I highlight three aspects:

1. non- and semi-terrestrial ecosystems;
2. ecosystem remnants, which are often relatively small, and raising the issue of spatial connections among remnants and among ecosystems in general; and,
3. species other than mammals and birds.

Type of interaction

My dissertation has focused on interactions involving the transfer of matter and energy. Input-output tables include transactions that do not involve such transfers, such as the provision of health or education services. Services are also transacted among species, in some case quite deliberately as discussed under mutualism in Chapter 3. The existence of 'engineering' networks based on niche construction has been raised in the literature (see Chapter 6). There is much information on habitat provision by one species to another, and it should be possible to construct engineering networks in some instances. However rules for network construction are required – it may not be as easy as with matter transfers. For example, niche construction by one species for the benefit of another may occur at the expense of a third. Should services and disservices be combined? Services will be easier to specify than disservices.

With the expansion of ecological networks beyond trophic interactions, integration of ecological and social interactions into one 'super' network becomes more complicated. Rules for network construction will also be required here.

Spatial extent

Spatial aspects in my analysis are limited to the relationship between species diversity and habitat availability. Topological network analysis is not explicit about the spatial nature of interactions. The method has been demonstrated for an essentially local issue where spatial extent and grain are the same. The method needs to be tested for larger areas comprising multiple ecosystems and multiple human communities. This poses particularly interesting challenges regarding spatial connections among ecosystems. The godwit, used to illustrate coevolution in Chapter 1, provides an interesting case. This migratory bird is dependent on habitat in the Netherlands for its breeding success, but on various ecosystems throughout Europe for its overall survival. It should be possible to

establish a socio-natural network for the godwit, to assess this species' potential for survival given the diversity of social impacts on its dependent ecosystems.

Addition of species

The addition of species to food webs was discussed in Chapters 4 and 5. Clearly there is still much to be learned about how food webs grow and how species enter ecological communities. Biotic exchange is the social impact that can lead to species' invading new ecosystems. The adverse impacts of such invasion include loss of species but also loss of income. Clearly this is an area of reciprocal impact between social and natural systems. As was shown in Chapter 6, biotic exchange is difficult to generalise, and the usefulness of topological network analysis was judged to be limited.

However, I would argue that further empirical research is needed. For example, known cases of invasion could be examined in terms of topological changes to food webs, and might suggest that certain combinations of species addition are either more prevalent, or that consistent changes in topology occur. Understanding of the topological changes that invasion triggers might provide better means for limiting its adverse impacts. A similar approach could be taken to instances where indirect effects, such as competition, moderate changes to an ecological community rather than direct species loss. Eutrophication is an example here, with its effects on competitive balances among basal species.

To conclude, I have developed a method and criterion for assessing future coevolution following human intervention into ecosystems. My focus has been on social impact, on biodiversity loss, and on local species extinction. It goes without saying that topological network analysis cannot be applied to all environmental management issues. Much environmental management in the Netherlands deals with the restoration of natural habitats, protection of endangered species, and reintroduction of locally extinct species. Topological network analysis is yet of limited use in such cases because the topological implications of species addition to networks are unclear, and because the principles guiding the development of engineering networks, reflecting habitat interactions, are not yet clear. Topological network analysis offers its greatest potential in cases where management choices revolve around differential extinction threats to species.

---

[1] The relevance of this quote to the chapter is much less self-explanatory than the quotes beginning other chapters. Readers of Terry Pratchett's Discworld books will recognise the quote, but perhaps will not understand its use here. Hence, an explanation ….of sorts.

There are various versions of the following story. A renowned physicist gave a lecture on the origins of the universe. Afterwards he was approached by an elderly woman who disagreed with him, arguing that the world rested on the back of an elephant that rested on the back of a turtle. The physicist smiled, rather superciliously, and asked what was under the turtle. The woman responded that the physicist might think himself very clever, but there was another turtle; didn't he realise that it is turtles all the way down.

Consequently the quote could suggest that the chapter deals with my 'cosmic view'.

Rather than Pratchett, I cite Geertz as the origin of the quote. Geertz likened the turtle to culture. When the anthropologist tries to explain a particular belief or value or practice, what she does is reveal a turtle – another belief or value or practice. Beneath that second turtle is a third belief or value or practice, and then another, ad infinitum. This is not to say that interpreting a bit of culture is futile, but that the task will never be complete; it will not be possible to capture all the meanings involved in a particular bit of culture. Instead, the best she can hope to do is to understand as much as she can about the various ways that belief or value or practice fits into its many contexts.

My use of this quote could be to liken culture to systems, and refer to the notion of nested systems – systems embedded in systems.

Other explanations are also possible.

Bibliography

Abrams, PA. 2000. The evolution of predator-prey interactions: theory and evidence. Ann rev. ecolog syst 31:79-105.

Adamic LA. 1999. The small world web. Res Adv Tech Digit Libr Proc 1696:442-452.

Adamic LA, BA Huberman, A-L Barabási, R Albert, H Jeong and G Bianconi. 2000. Power-law distribution of the world wide web. Science 287:2115.

Adams DC and FJ Rohlf. 2000. Ecological character displacement in Plethodon: Biomechanical differences found from a geometric morphometric study. Proc Natl Acad Sci USA 97:4106-4111.

Adger WN. 1999. Evolution of economy and environment: an application to land use in lowland Vietnam. Ecol Econ 31:365-379.

Agrawal AA. 2000. Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. Trends Plant Sci 5:309-313.

Ahmad YJ, El Serafy S and Lutz E. (eds) 1989. Environmental Accounting for Sustainable Development. The World Bank, Washington DC.

Albert R and A-L Barabási. 2002. Statistical mechanics of complex networks. Rev Mod Phys 74:47-97.

Albert R, H Jeong and A-L Barabási. 2000. Error and attack tolerance of complex networks. Nature 406:378-382.

Allaby M. 1998. Dictionary of Ecology. 2nd edition. Oxford University Press, Oxford.

Allen TFH and TB Starr. 1982. Hierarchy: perspectives for ecological complexity. University of Chicago Press, Chicago, Illinois, USA.

Alon U, MG Surette, N Barkai and S Leibler. 1999. Robustness in bacterial chemotaxis. Nature 397:168-171.

Amaral R, A Scala, M Barthelmy and HE Stanley. 2000. Classes of small-world networks. Proc Natl Acad Sci USA 97:11149-11152.

Amblers J W and J BR Alcala-Herrera. 1994. Trophic roles of particle feeders and detritus in a mangrove island prop root ecosystem. Hydrobiologia 292-293:437-446.

Andelman SJ and WF Fagan. 2000. Umbrellas and flagships: Efficient conservation surrogates or expensive mistakes? Proc Natl Acad Sci USA 97:5954-5959.

Andrén H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: A review. Oikos 71:355-366.

Archetti M. 2000. The Origin of Autumn Colours by Coevolution. J Theor Biol 205:624-630.

Argyris C and DA Schön, 1978. Organizational Learning: A Theory of Action Perspective. Addison-Wesley, Reading, Massachusetts.

Arroyo CA. 1979. Flora of the Philippines Mangrove. Flora of the Philippines Mangrove 10:33-44.

Axelrod R. 1984. The Evolution of Cooperation. Basic Books Inc, New York.

Axelrod R and WD Hamilton. 1981. The evolution of cooperation. Science 211:1390-1396.

Axtell R and JM Epstein. 1999. Coordination in transient social networks: an agent-based computational model of the timing of retirement. In: HJ Aaron (ed) Behavioral Dimensions of Retirement Economics. Brookings Institute, Washington, DC, p 161-183.

Ayres RU and I Gutmanis. 1972. Technological change, pollution and treatment cost coefficients in Input0Output analysis. In: RG Ridker (ed) Population, Resources and the Environment. Commission on Population Growth and the American Future, US Government Printing Office, Washington DC.

Bak P. 1996. How Nature Works: The Science of Self-Organised Criticality. Copernicus (an imprint of Springer-Verlag New York, Inc), New York, 212 pp.

Bak P, C Tang and K Wiesenfeld. 1988. Self-organized criticality. Phys Rev A 38:364-374.

Barabási A-L and R Albert. 1999. Emergence of scaling in random networks. Science 286:509-512.

Barbault R, RK Colwell, B Dias, DL Hawksworth, M Hoston, P Lasserre, D Stone and T Younes. 1991. Conceptual framework and research and research issues for species diversity at the community level. In: Solbrig OT (ed) From Genes to Ecosystems: a Research Agenda for Biodiversity. IUBS, Cambridge, Mass, p 37–71

Barbier EB. 1987. The concept of sustainable economic development. Environ Conserv 14:101-110.

Barth FG. 1991. Insects and Flowers: The Biology of a Partnership. Princeton University Press, Princeton, New Jersey.

Barthélémy M and LAN Amaral. 1999. Small-world networks: evidence for a crossover picture. Phys Rev Lett 82:3180-3183.

Barton NH. 2001. Speciation. Trends Ecol Evol 16:325.

Beissinger SR. 2000. Ecological mechanisms of extinction. Proc Natl Acad Sci USA 97:11688-11689.

Benkman CW. 1999. The selection mosaic and diversifying coevolution between crossbills and lodgepole pine. Am Nat 153 Supplement:S75-S91.

Bennagen E and D Cabahug. 1992. Mangrove forest accounting: physical accounts. The Philippine Natural Resources Accounting Project (NRAP Phase 1, Technical Appendices). Manila.

Bergh JCJM van den. 2005. Evolutionary Analysis of Economic Growth, Environmental Quality and Resource Scarcity. In: RU Ayres, D Simpson and M Toman (eds). Scarcity and Growth in the New Millennium. Resources for the Future, Washington DC, pp 177-197.

Bergh JCJM van den, A Faber, AM Idenburg and FH Oosterhuis. 2006. Survival of the greenest: Evolutionary economics and policies for energy innovation. Environmental Sciences 3: 57-71.

Bergh JCJM van den and J Gowdy. 2000. Evolutionary theories in environmental and resource economics: approaches and applications. Environ Resour Econ 17:37– 52.

Bergh JCJM van den and S Stagl. 2003. Co-evolution of economic behaviour and institutions: towards a theory of institutional change. J Evol Econ 13:289– 317.

Bertalanffy L von. 1968. General System Theory: Foundations, Development, Applications. George Braziller, New York.

Bertalanffy L von. 1975. Perspectives on General Systems Theory. George Braziller, New York.

Bond WJ. 1993. Keystone species. In: ED Schulze and HA Mooney (eds) Biodiversity and ecosystem function. Springer, New York Heidelberg Berlin, p 237–291.

Bonsall MB and TH Jones. 1998. Determinants of dynamics: population size, stability and persistence. Trends Ecol Evol 15:174-176.

Borrvall C, B Ebenham and T Jonsson. 2000. Biodiversity lessens the risk of cascading extinction in model food webs. Ecol Lett 3:131-136.

Bouillon S, N Koedam, A Raman and F Dehairs. 2002. Primary producers sustaining macroinvertebrate communities in intertidal mangrove forests. Oecologia, 130:441-448.

Brembs B. 1996. Chaos, cheating and cooperation: potential solutions to the prisoner's dilemma. Oikos 76:14-24.

Bronstein JL. 1994. Conditional outcomes in mutualistic interactions. Trends Ecol Evol 9:214-217.

Brooks TM, SL Pimm and NJ Collar. 1997. The extent of deforestation predicts the number of birds threatened with extinction in insular South-east Asia. Conserv Biol 11:382-394.

Brown JL. 1983. Cooperation: a biologist's dilemma. Adv Stud Behav 13:1-37.

Bruyn SM de, JCJM van den Bergh and JB Opschoor. 1998. Economic Growth and Emissions: Reconsidering the Empirical Basis of Environmental Kuznets Curves. Ecol Econ 25:161-177.

Bshary R and R Noë. 2000. Anti-predation behaviour of red colobus monkeys in the presence of chimpanzees. Behav Ecol Sociobiol 41:321-333.

Buddemeier RW and SV Smith. 1988. Coral reef research in an era of rapidly rising sea level: predictions and suggestions for long-term research. Coral Reefs 7:51-56.

Burdon JJ and PH Thrall. 1999. Spatial and temporal patterns in coevolving plant and pathogen associations. Am Nat 153 Supplement:S15-S33.

Burton I, S Huq, B Lim, O Pilifosova and EL Schipper. 2002. From impacts assessment to adaptation priorities: the shaping of adaptation policy. Climate Policy 2:145-159.

Caldarelli G, PG Higgs and AJ McKane. 1998. Modelling Coevolution in Multispecies Communities. J Theor Biol 193:345-358.

Callaway DS, MEJ Newman, SH Strogatz and DJ Watts. 2000. Network robustness and fragility: percolation on random graphs. Phys Rev Lett 85:5468-5471.

Calumpong HP. 1994. Status of mangrove resources in the Philippines. In: CR Wilkinson, S Sudara and CL Ming (eds) Proceedings of the 3rd ASEAN-Australia Symposium on Living Coastal Resources, May 16-20, 1994. Chulalongkorn University, Bangkok, Thailand Chulalongkorn University, Bangkok, Thailand, 16-20 May 1994.

Camacho J, R Guimerà and LAN Amaral. 2002. Analytical solution of a model for complex food webs. Phys Rev E 65:art no 030901.

Cameron T. 2002. 2002: the year of the 'diversity-ecosystem function' debate. Trends Ecol Evol 17:495-496.

Carandang A and JE Padilla. 1997. Assessment of forest resources of the Pagbilao mangrove forest. In: R Janssen and JE Padilla (eds) Mangroves or Fishponds? Valuation and Evaluation of

Management Alternatives for the Pagbilao Mangrove Forest. Resources, Environment and Economics Centre for Studies Inc, Pasig City, Philippines and Institute for Environmental Studies (IVM), Vrije Universiteit, Amsterdam, The Netherlands.

Carpenter SR. 2002. Ecological futures: building an ecology of the long now. Ecology: 83:2069–2083.

Carpenter SR. 2003. Regime Shifts in Lake Ecosystems: Pattern and Variation. Excellence in Ecology Series 15. Oldendorf/Luhe, Germany: Ecol Inst.

Chapela IH, SA Rehner, TR Schulz and UG Mueller. 1994. Evolutionary history of the symbiosis between fungus-growing ants and their fungi. Science 266:1691-1694.

Chapin FSI, ES Zaveleta, ES Eviner, RL Naylor, PM Vitousek, HL Reynolds, DU Hooper, S Lavorel, OE Sala, SE Hobbie, MC Mack and S Diaz. 2000. Consequences of changing biodiversity. Nature 405:234-242.

Cohen JE. 1989. Just proportions in food webs. Nature 341:104-105.

Cohen JE, F Briand and CM Newman. 1990. Community Food Webs: Data and Theory, Springer-Verlag, Berlin 300 pp.

Cohen AN and JT Carlton. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279:555-558.

Cohen JE. 1989. ECOWeB - Machine-readable Database of Food Webs. Rockefeller University, New York.

Colding J and C Folke. 1997. The relations among threatened species, their protection and taboos. Conservation Ecology [online]1(1): 6. Available from the Internet URL: http://www.consecol.org/vol1/iss1/art6/

Collie J, K Richardson and J Steele. 2004. Regime shifts: can ecological theory illuminate the mechanisms? Prog Oceanogr 60:281-301.

Connor R. 1995. The benefits of mutualism: a conceptual framework. Biol Rev 70:427-457.

Craig JV and WM Muir. 1996. Group selection for adaptation to multiple-hen cages: beak-related mortality, feathering and body weight responses. Poult Sci 75:294-302.

Crooks JA and ME Soule. 1999. Lag times in population explosions of invasive species: causes and implications. In: OT Sandlund, PJ Schei and A Viken (eds) Invasive Species and Biodiversity Management. Kluwer, Dordrecht, the Netherlands, p 103-125.

Cury P, A Bakun, RJ Crawford, A Jarre, RA Quinones, LJ Shannon and H M Verheye. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in "wasp - waist" ecosystems. ICES J Mar Sci 57:603-618.

Cushman JH and JF Addicott. 1991. Conditional interactions in ant-plant-homopteran mutualisms. In: CR Huxley and DF Cutler (eds) Ant-Plant Interactions. Oxford University Press, Oxford, p 92-103.

Cushman JH and TG Whitham. 1989. Conditional mutualism in a membracid-ant association: temporal, age-specific and density-dependent effects. Ecology 70:1040-1047.

Cushman JH and TG Whitham. 1991. Competition mediating the outcome of a mutualism: protective services of ants as a limiting resource for membracids. Am Nat 138:851-865.

Darwin Ch. 1859. The Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life. John Murray, London.

Darwin Ch. 1871. The Descent of Man and Selection in Relation to Sex. John Murray, London.

David PA and GS Rothwell. 1996. Standardization, diversity and learning: strategies for the coevolution of technology and industrial capacity. Int J Ind Organ 14:181-201.

Dawkins R and JR Krebs. 1979. Arms races between and within species. P Roy Soc Lond B Bio 205:489-511.

DeAngelis D. 1975. Stability and connectance in food web models. Ecology 56:238-243.

DENR 2003. Revised Master Plan for Forestry. Philippines Department of Environment and Natural Resources, The Philippines.

Diamond J. 1986. Evolution of ecological segregation in the New Guinea montane avifauna. in J Diamond and TJ Case (eds) Community Ecology. Harper & Row, New York, p 98-125.

Diaz HF, JK Eischeid, C Duncan and RS Bradley. 2003. Variability of freezing levels, melting season indicators, and snow cover for selected high-elevation and continental regions in the last 50 years, Clim Change 59:33– 52.

Didham RK, JH Lawton, PM Hammond and P Eggleton. 1998. Trophic structure stability and extinction dynamics of beetles (Coleoptera) in tropical forest fragments. Phil Trans R Soc Lond B 353, 437–451.

Dorfman R, P Samuelson and R Solow. 1958. Linear Programming and Economic Analysis. McGraw Hill, New York.

Duffy JE. 2003. Biodiversity loss, trophic skew and ecosystem functioning. Ecol Lett 6: 680-687(8).

Dunne JA, U Brose, RJ Williams and ND Martinez. 2005. Modelling food-web dynamics: complexity-stability implications. In: A Belgrano, UM Scharler, JA Dunne and RE Ulanowicz (eds) Aquatic Food Webs: An ecosystem approach. Oxford University Press, Oxford.

Dunne JA, RJ Williams and ND Martinez. 2002a. Food-web structure and network theory: the role of connectance and size. Proc Natl Acad Sci USA 99:12917-12922.

Dunne JA, RJ Williams and ND Martinez. 2002b. Network structure and biodiversity loss in food webs: robustness increases with connectance. Ecol Lett 5:558-567.

Dunne JA, RJ Williams, and ND Martinez. 2004. Network structure and robustness of marine food webs. Marine Ecology Progress Series 273:291-302.

Edmonds B. 1999. What is complexity? - The philosophy of complexity per se with application to some examples in evolution. In: F Helighen, J Bollen and A Riegler (eds) The Evolution of Complexity. Kluwer Academic Publishers, Dordrecht, p 1-16.

Ehrlich P and P Raven. 1964. Butterflies and plants: a study in coevolution. Evolution 18:586-608.

Ehrlich PR. 2001. Intervening in evolution: ethics and actions. Proc Natl Acad Sci USA 98:5477-5480.

Elton CS. 1927. Animal Ecology. Macmillan, New York.

Elton CS. 1958. The Ecology of Invasions by Animals and Plants. Chapman & Hall, London.

Erwin DH. 2001. Lessons from the past: Biotic recoveries from mass extinctions. Proc Natl Acad Sc. USA 98:5399-5403.

Farber S. 1991. Local and global incentives for sustainability: failures in economic systems. In: R Costanza (ed) Ecological Economics: The Science and Management of Sustainability. Columbia University Press, New York, p 322-354.

Fiorillo F. 2001. Rate of growth and sector specialisation coevolution in a Kaldorian export-led growth model. Struct Change Econ Dynam 12:91-114.

Folmer H. and A de Zeeuw. 1999. Game theory in environmental policy analysis. In: JCJM van der Bergh (ed) Handbook of Environmental and Resource Economics. Edward Elgar, Cheltenham, UK, p 1089-1098.

Foster J. 1997. The analytical foundations of evolutionary economics: from biological analogy to economic self-organisation. Struct Change Econ Dynam 8:427-451.

Francis RC and SR Hare. 1994. Decadal-scale regime shifts in the large marine ecosystems of the North-east Pacific: a case for historical science. Fish Oceanogr 3:279-291.

Freeman S and JC Herron. 1998. Evolutionary Analysis. Prentice Hall, Upper Saddle River, New Jersey.

Futuyma D. 1998. Evolutionary Biology. Third Edition. Sinaauer Associates Inc, Sunderland, Massachusetts.

Futuyma DJ and M Slatkin. 1983. Introduction. In: DJ Futuyma and M Slatkin (eds) Coevolution. Sinauer Associates Inc, Sunderland, Massachusetts, p 1-13.

Gadgil M and F Berkes. 1991. Traditional resource management systems. Resour Manage Opt 8: 127-141.

Garcia EA. 1999. The use of complex adaptive systems in organisational studies. In: F Helighen, J Bollen and A Riegler (eds) The Evolution of Complexity. Kluwer Academic Publishers, Dordrecht, p 281-306.

García-Pedrajas N, C Hervás-Martínez and J Muñoz-Pérez. 2002. Multi-objective cooperative coevolution of artificial neural networks (multi-objective cooperative networks). Neural Networks 15:1259-1278.

Gardner MR and WR Ashby. 1970. Connectance of large dynamical (cybernetic) systems: critical values for stability. Nature 228:784.

Geertz C. 1973. The Interpretation of Cultures. Basic Books, New York.

Gell-Mann M. 1995. What Is Complexity? Complexity 1.

Gilbert AJ and R Janssen. 1998. Use of environmental functions to communicate the values of a mangrove ecosystem under different management regimes. Ecol Econ 25:323-346.

Gilbert AJ, M van Herwijnen and CM Lorenz. 2004. From spatial models to spatial evaluation in the analysis of wetland restoration in the Vecht river basin. Regional Environmental Change 4:118–131.

Gilbert F, A Gonzalez A and I Evans-Freke. 1998. Corridors maintain species richness in the fragmented landscapes of a microecosystem. Proc R Soc Lond B 265, 577–582.

Gitay H, S Brown, W Easterling, B Jallow, J Antle, M Apps, R Beamish, T Chapin, W Cramer, J Frangi, J Laine, E Lin, J Magnuson, I Noble, J Price, T Prowse, T Root, E Schulze, O Sirotenko, B Sohngen, J Soussana. 2001. Ecosystems and their goods and services. In: JJ McCarthy, OF Canziani, NA Leary, DJ Dokken and KS White (eds) Climate Change 2001: Impacts, Adaptation and Vulnerabilty. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Published for the IPCC by Cambridge University Press, Cambridge, p 235-342.

Glantz MH. 1986. Man, state and fisheries: an inquiry into some societal constraints that affect fisheries management. Ocean Dev Int Law 17:191-346.

Gonzalez A, JH Lawton, FS Gilbert, TM Blackburn and I Evans-Freke. 1998. Metapopulation dynamics, abundance and distribution in a microecosystem. Science 281:2045-2047.

Goodnight CJ. 1990a. Experimental studies of community evolution. I: The response to selection at the community level. Evolution 44:1624.

Goodnight CJ. 1990b. Experimental studies of community evolution. II: The ecological basis of the response to community selection. Evolution 44:1625-1636.

Goodnight CJ. 2000. Heritability at the ecosystem level. Proc Natl Acad Sc. USA 97:9265-9366.

Goodnight CJ and L Stevens. 1997. Experimental studies of group selection: What do they tell us about group selection in nature? Am Nat 150:S59-S79.

Gould SJ and EA Lloyd. 1999. Individuality and adaptation across levels of selection: How shall we name and generalize the unit of Darwinism? Proc Natl Acad Sc. USA 96:11904-11909.

Gowdy JM. 1994. Coevolutionary Economics. The Economy, Society and the Environment. Kluwer Scientific Publishers, Dordrecht.

Graham R and E Lundelius Jr. 1984. Coevolutionary disequilibrium and Pleistocene extinctions. In: P Martin and R Klein (eds) Quaternary Extinctions. University of Arizona Press, Tuscon, p 223-249.

Grant BR and PR Grant. 1989. Evolutionary Dynamics of a natural population: the large cactus finch of the Galápagos. University of Chicago Press, Chicago.

Grant PR. 1986. Ecology and Evolution of Darwin's Finches. Princeton University Press, Princeton.

Grant PR. 1994. Ecological character displacement. Science 266:746-747.

Grant PR and BR Grant. 2002. Adaptive Radiation of Darwin's Finches: recent data help explain how this famous group of Galápagos birds evolved, although gaps in our understanding remain. Am Sci 90.

Grayson DK. 2001. The archaeological record of human impacts on animal populations. J World Prehist 15:1-68.

Groot RS de. 1992. Functions of Nature: evaluation of nature in environmental planning, management and decision-making. Wolters Noordhoff BV, Groningen, the Netherlands, 345 pp.

Grosholz E. 2002. Ecological and evolutionary consequences of coastal invasions. Trends Ecol Evol 17:22-27.

Gunderson LH, CS Holling and SS Light. 1995. Barriers broken and bridges built. In: LH Gunderson, CS Holling and SS Light (eds) Barriers and bridges to the renewal of ecosystems and institutions. Columbia University Press, New York, p 489-532.

Haitzer M, GR Aiken and JN Ryan. 2002. Binding of mercury (II) to dissolved organic matter: the role of the mercury-to-DOM concentration ratio. Environ Sci Technol 36:3564-3570.

Harbaugh W, A Levinson and D Wilson. 2000. Re-examining the Evidence for an Environmental Kuznets Curve. NBER Working Paper No 7711, National Bureau of Economic Research, Cambridge, MA.

Hedenström A and M Rosén. 2001. Predator versus prey: on aerial hunting and escape strategies in birds. Behav Ecol 12:150-156.

Helighen F. 1999. The growth of structural and functional complexity during evolution. In: F Helighen, J Bollen and A Riegler (eds) The Evolution of Complexity. Kluwer Academic Publishers, Dordrecht, p 17-44.

Herre EA, N Knowlton, UG Mueller and SA Rehner. 2000. The evolution of mutualisms: exploring the paths between conflict and cooperation. Trends Ecol Evol 14:49-53.

Heywood VH. 1989. Patterns, Extents and Modes of Invasions by Terrestrial Plants. In: JA Drake, HA Mooney, F di Castri, RH Groves, FJ Kruger, M Rejmánek and M Williamson (eds) Biological Invasions: A Global Perspective. SCOPE 37, John Wiley & Sons Ltd, Chichester, UK.

Hinckle G, JK Wetterer, TR Schulz and ML Sogin. 1994. Phylogeny of the attine ant fungi based on analysis of small subunit ribosomal RNA gene sequences. Science 266:1695-1697.

Hodgson G. 1993. Economics and Evolution. Bringing life back into economics. Cambridge, UK and Ann Arbor, MI, Polity Press and University of Michigan Press.

Hodgson GM. 2002. Darwinism in economics: from analogy to ontology. J Evol Econ 12:259-281.

Holland JH. 1995. Hidden Order: How Adaptation Builds Complexity. Helix Books, Reading, Massachusetts.

Holling CS. 1973. Resilience and stability of ecological systems. Ann Rev Ecolog Syst.4:1-23.

Holling CS. 1978. Adaptive Environmental Assessment and Management. John Wiley & Sons, New York.

Holling CS. 1986. The resilience of terrestrial ecosystems: local surprise and global change. In: CW Clark and RE Munn (eds) Sustainable Development of the Biosphere. Cambridge University Press, Cambridge, p 292-317.

Holling CS. 1996. Engineering resilience versus ecological resilience. In: P Schulze (ed) Engineering within Ecological Constraints. National Academy Press, Washington, DC, p 31-44.

Holling CS. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. Ecol Monogr 62:447-502.

Holtz-Eaken D and T Selden. 1995. Stoking the fires? CO2 emissions and economic growth. J Public Econ 57:85-101.

Hooper DU and PM Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. Science 277:1305.

Hosper H. 1997. Clearing lakes and ecosystem approach to the restoration and management of shallow lakes in the Netherlands. PhD Thesis, Agricultural University of Wageningen, Wageningen, the Netherlands.

Houghton JT, LG Meiro Filho, BA Callandar, N Harris, A Kattenberg, K Maskell (eds) 1996. Climate Change 1995: The Science of Climate Change. Cambridge University Press, Cambridge, 285 pp.

http://www.arcbc.org.ph/ last visited on 4 July 2006.

http://www.birdwatch.ph/ last visited on 4 July 2006.

http://www.fishbase.org/search.php last visited on 4 July 2006.

http://marinefisheries.org last visited on 4 July 2006.

http://www.mesa.edu.au/habitat/chall04.asp#top last visited on 4 July 2006.

Huberman BA and LA Adamic. 1999. Growth dynamics of the World-Wide Web. Nature 401:131.

Huberman BA, PLT Pirolli, JE Pitkow and RJ Lukose. 1999. Strong regularities in world wide web surfing. Science 280:95-97.

Huston MA, LW Aarssen, MP Austin, BS Cade, JD Fridley, E Garnier, JP Grime, J Hodgson, WK Lauenroth, K Thompson, JH Vandermeer and DA Wardle. 2002. No Consistent Effect of Plant Diversity on Productivity. Science 289:1255.

IMBER. 2005. Science Plan and Implementation Strategy. IGBP Report No 52, IGBP Secretariat, Stockholm, 76pp.

IPCC. 2001. Impacts, Adaptation and Vulnerability, Summary for Policymakers and Technical Summary of the Working Group II Report. IPCC, Geneva.

Jablonski D. 2001. Lessons from the past: Evolutionary impacts of mass extinctions. Proc Natl Acad Sc. USA 98:5393-5398.

Jackson JBC. 2001. What was natural in the coastal oceans? Proc Natl Acad Sc. USA 98:5458-5465.

Jain S and S Krishna. 2002. Large extinctions in an evolutionary model: The role of innovation and keystone species. Proc Natl Acad Sc. USA 99:2055-2060.

James DE, J Chambers, AJ Gilbert and H Wright. 1983. An Integrated Energy-Economic-Environmental Model for Australia. Centre for Environmental and Urban Studies, Macquarie University, North Ryde, Australia. Prepared for the National Energy Research, Development and Demonstration Council, 539 pp.

James DE. 1980. A system of energy accounts for Australia. Econ Rec 56:171-181.

Janssen M (ed) 2002. Complexity and Ecosystem Management: The Theory and Practice of Multi-agent Systems. Edward Elgar, Cheltenham, UK.

Janssen M and E Ostrom. 2005. Governing social-ecological systems. In: KL Judd and L Tesfatsion (eds) Handbook of Computational Economics II: Agent-based Computational Economics. North-Holland, Amsterdam.

Janssen R. 1992.Multiobjective Decision Support for Environmental Management. Kluwer Academic Publishers, Dordrecht.

Janssen R. and M van Herwijnen. 2006. DEFINITE 3.1. A system to support decisions on a finite set of alternatives (Software package and user manual) Institute for Environmental Studies (IVM), Vrije Universiteit, Amsterdam.

Janssen R and JE Padilla (eds). 1997. Mangroves or fishponds? Valuation and evaluation of management alternatives for the Pagbilao mangrove forest. Final report. Resources, Environment and Economics Centre for Studies Inc., Pasig City, Philippines and Institute for Environmental Studies (IVM), Vrije Universiteit, Amsterdam, The Netherlands.

Janssen R and JE Padilla. 1999. Preservation or conversion? Valuation and evaluation of a mangrove forest in the Philippines. Environ Resour Econ 14:297-331.

Janzen, DH. 1997. A Caricature of Seed dispersal by Animal Guts. Oxford Press, Oxford.

Jeong H. 2003. Complex scale-free networks. Physica A 321:226-237.

Jeong H, B Tombor, R Albert, ZN Oltvai and A-L Barabási. 2000. The large-scale organization of metabolic networks. Nature 407:651-654.

Jeong H, SP Mason, A-L Barabási and ZN Oltvai. 2001. Lethality and centrality in protein networks. Nature 411:41.

Jones CG, JH Lawton and M Shachak. 1994. Organisms as ecosystem engineers. Oikos 69:373-386.

Jordán F and I Scheuring. 2002. Searching for keystones in ecological networks. Oikos 99:607-612.

Jordano P, J Bascompte and JM Olesen. 2003. Invariant properties in coevolutionary networks of plant-animal interactions. Ecol Lett 6:69-81.

Jørgensen BB and K Richardson (eds) 1996. Eutrophication in Coastal Marine Ecosystems. American Geophyiscal Union, Washington DC, 272 pp.

Kaiser J. 2000. Rift over biodiversity divides ecologists. Science 289:1282-1283.

Kattenberg A, F Giorgi, H Grass, GA Meehl, JFB Mitchell, RJ Stouffer, T Tokioka, AJ Weaver and TML Wigley. 1996. Climate Models - Projections of Future Climate. In: JT Houghton, LG Meiro Filho, BA Callandar, N Harris, A Kattenberg and K Maskell K (eds) Climate Change 1995: The Science of Climate Change. Cambridge University Press, p 285-387.

Kauffman SA. 1993. The Origins of Order: self-organization and selection in evolution. Oxford University Press, Oxford.

Kauffman SA. 1995. At Home in the Universe. Oxford University Press, Oxford.

Kay JJ, HA Regier, M Boyle and G Francis. 1999. An ecosystem approach for sustainability: addressing the challenge of complexity. Future 31:721-742.

Kirchner JW. and A Weil. 2000. Delayed biological recovery from extinctions throughout the fossil record. Nature 404:177-180.

Kleypas JA, RW Buddemeier, D Archer, J Gattuso, C Landon and BN Opdike, 1999. Geochemical consequences of increased carbon dioxide in coral reefs. Science 284:118-120.

Knowlton N. 2001. The future of coral reefs. Proc Natl Acad Sc. USA 98:5419-5425.

Kochen M (ed). 1989. The Small World. Ablex, Norwood, New Jersey.

Kraaijeveld AR and HCJ Godfray. 1999. Geographic patterns in the evolution of resistance and virulence in Drosophila and its parasitoids. Am Nat 153 Supplement:S61-S74.

Labandeira CC, DL Dilcher, DR Davis and DL Wagner. 1994. Ninety-seven million years of angiosperm-insect association: paleobiological insights into the meaning of coevolution. Proc Natl Acad Sc. USA 91:12278-12282.

Lago-Fernandez LF, R Huerta, F Corbacho and JA Siguenza. 2000. Fast Response and Temporal Coherent Oscillations in Small-World Networks. Phys Rev Lett 84:2758-2761.

Laland KN, FJ Odling-Smee and MW Feldman. 1999. Evolutionary consequences of niche construction and their implications for ecology. Proc Natl Acad Sc. USA 96:10242–47.

Laurance WF. 2000. Do edge effects occur over large spatial scales? Trends Ecol Evol 15:134-135.

Lawton JH. 1995. Population dynamic principles. In: JH Lawton and RM May (eds) Extinction Rates. Oxford University Press, Oxford, p 146–163.

Lee CE. 2002. Evolutionary genetics of invasive species. Trends Ecol Evol 17:386-391.

Lee K. 1993. Compass and Gyroscope: Integrating Science and Politics for the Environment. Island Press, Washington, DC.

Lee SY. 1999. Tropical mangrove ecology: Physical and biotic factors influencing ecosystem structure and function. Aust J Ecol 24:355-366.

Leeuw SE van der and C Aschan-Leygonie. 2000. A long-term perspective on resilience in socio-natural systems. Abisko, Sweden, May 22-26, 2000.

Legler J. 2001. Development and application of in vitro and in vivo reporter gene assays for the assessment of (xeno-)estrogenic compounds in the aquatic environment. PhD Dissertation, Wageningen University , The Netherlands, 132 pp.

Leontief W. 1936. Quantitative input and output relations in the economic system of the United States. Rev Econ Stat XVIII:105-125.

Leontief W. 1941. The Structure of the American Economy, 1919-1929. Harvard University Press, Cambridge, Massachusetts.

Leontief W. 1966. Input-Output Economics. Oxford University Press, New York.

Leontief W and D Ford. 1972. Air pollution and the economic structure: empirical results of Input-Output computations. In: A Brody and AP Carter (eds) Input-Output Techniques. North-Holland Publishers, Amsterdam.

Levin S. 1999. Fragile Dominion: Complexity and the Commons. Perseus Publishing, Cambridge, Massachusetts.

Levinton JS. 1982. The body size prey size hypothesis - the adequacy of body size as a vehicle for character displacement. Ecology 63:869-872.

Limburg KE, RV O'Niell, R Costanza and S Farber. 2002. Complex systems and valuation. Ecol Econ 41:409-420.

Lin CK. 1989. Prawn culture in Taiwan. What went wrong? World Aquaculture 20:19-20.

Lindgren K and MG Nordahl. 1994. Evolutionary dynamics of spatial games. Physica D 75:292-309.

Linhart YB. 1999. Mosaic landscapes, family structure and evolution. Trends Ecol Evol 14:376-377.

Lively CM. 1999. Migration, virulence and the geographic mosaic of adaptation by parasites. Am Nat 153 Supplement:S34-S47.

Looy CV, WA Brugman, DL Dilcher and H Visscher. 1999. The delayed resurgence of equatorial forests after the Permian-Triassic crisis. Proc Natl Acad Sc. USA 96: 13857-13862.

Loreau M, S Naeem, P Inchausti, J Bengtsson, JP Grime, A Hector, DU Hooper, MA Huston, D Raffaelli, B Schmid, D Tilman and DA Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. Science 294:804-808.

Lorenzoni I, A Jordan, M Hulme, RK Turner and T O'Riordan. 2000a. A co-evolutionary approach to climate change impact assessment - Part I: Integrating socio-economic and climate change scenarios. Global Environ Chang 10:57-68.

Lorenzoni I, A Jordan, T O'Riordan, RK Turner and M Hulme. 2000b. A co-evolutionary approach to climate change impact assessment - Part II: A scenario-based case study in East Anglia (UK). Global Environ Chang 10:145-155.

MacArthur RH. 1955. Fluctuation of animal populations and a measure of community stability. Ecology 36:533-536.

Macintosh D. J., E. C. Ashton, and S. Havonon, 2001. Mangrove Rehabilitation and Intertidal Biodiversity: a Study in the Ranong Mangrove Ecosystem, Thailand. Estuarine, Coastal and Shelf Science, 55**:**331-345.

Mack AL. 2000. Did fleshy fruit pulp evolve as a defence against seed loss rather than as a dispersal mechanism? J Bioscience 25:93-97.

Mackenzie FT, LM Ver and A Lerman. 2002. Century-scale nitrogen and phosphorus controls of the carbon cycle. Chem Geol 190 :13-32.

Margoluis R and N Salafsky. 1998. Measures of Success: Designing, Managing and Monitoring Conservation and Development Projects. Island Press, Washington, DC.

Martinez ND. 1991. Artifacts or attributes? Effects of resolution on the Little Rock Lake food web. Ecol Monogr 61:367-392.

Martinez ND. 1992. Constant connectance in community food webs. Am Nat 139:1208-1218.

Maslov S and K Sneppen. 2002. Specificity and stability in topology of protein networks. Science 296:910-913.

May RM. 1972. Will a large complex system be stable? Nature 238:413-414.

May RM. 1973. Stabiliity and Complexity in Model Ecosystems. Princeton University Press, Princeton, New Jersey.

May RM. 1975. Patterns of species abundance and diversity. In: ML Cody and JM Diamond (eds) Ecology and evolution of communities. Harvard University Press, Cambridge, Massachusetts, p 81-120.

May RM. 1983. The structure of food webs. Nature 301:566-568.

May RM. 1988. How many species are there on Earth? Science 241:1441-1449.

Mayr E. 1997. The objects of selection. Proc Natl Acad Sc. USA 94:2094.

McCann K. 2000. The diversity–stability debate. Nature 405:228-233.

McCann K, A Hastings and GR Huzel. 1998. Weak trophic interactions and the balance of nature. Nature 395:794-798.

McCarthy JJ, OF Canziani, NA Leary, DJ Dokken and KS White KS (eds) 2001. Climate Change 2001: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Third

Assessment Report of the Intergovernmental Panel on Climate Change (IPCC), New York, Cambridge University Press.

McGlade J. 1995. Archaeology and the ecodynamics of human modified landscapes. Antiquity 69, 113-132.

McLean RF, A Tsyban, V Burkett, JO Codignotto, DL Forbes, N Mimura, RJ Beamish, V Ittekkot. 2001. Coastal zones and marine ecosystems. In: JJ McCarthy, OF Canziani, NA Leary, DJ Dokken and KS White (eds) Climate Change 2001: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Published for the IPCC by Cambridge University Press, Cambridge, p 343-416.

Mee LD. 2004. Assessment and monitoring requirements for the adaptive management of Europe's seas. In: J Vermaat, L Bouwer, RK Turner and W Salomons (eds) Managing European Coasts: Past Present and Future. Springer Verlag, Berlin.

Melián CJ and J Bascompte. 2002. Complex networks: two ways to be robust? Ecol Lett 5:705-708.

Mendel G. 1866. Versuche uber Pflanzenhybriden (Experiments in Plant Hybridisation). Oliver and Boyd, London (English translation published in 1965).

Metzger J and H Décamps. 1997. The structural connectivity threshold: An hypothesis in conservation biology at the landscape scale. Acta Oecol 18:1-12.

Michalakis Y, I Olivier, F Renaud and M Raymond. 1992. Pleitropic action of parasites: how to be a good host. Trends Ecol Evol 7:59-62.

Micheli F. 1999. Eutrophication, Fisheries and Consumer-Resource Dynamics in Marine Pelagic Ecosystems. Science 285:1396-1398.

Milgram S. 1967. The small world problem. Psychol Today 2:60-67.

Millenium Ecosystem Assessment. 2003. Ecosystems and Human Well-Being: A Framework for Assessment. Island Press, Washington, DC.

Miller JH. 1996. The coevolution of automata in the repeated prisoner's dilemma. J Econ Behav Organ 29:87-112.

Mills LS, ME Soule and DF Doak. 1993. The keystone-species concept in ecology and conservation. Bioscience 43:219–224.

Montoya JM and RV Solé. 2002. Small world pattern in food webs. J Theor Biol. 214:405-412.

Mooney HA and EE Cleland. 2001. The evolutionary impact of invasive species. Proc Natl Acad Sc. USA 98:5446-5451.

Mosqueira I, PR Estrada and L Brookshaw. 1999. Hydrodynamical simulations of narrow planetary rings. I: Scaling. Icarus 139:260-285.

Muir WM. 1996. Group selection for adaptation to multiple-hen cages: selection program and direct responses. Poultry Sci 75:447-458.

Munro AM. 1997. Economics and biological evolution. Environ Resour Econ 9:429-229.

Muradian R. 2001. Ecological thresholds: a survey. Ecol Econ 38:7-24.

Murphy P. 2000. Symmetry, contingency, complexity: Accommodating uncertainty in public relations theory. Public Relat Rev 26:447-462.

Myers N and AH Knoll. 2001. The biotic crisis and the future of evolution. Proc Natl Acad Sc. USA 98:5389-5392.

Myers N. 1997. Marine fisheries: two macro-constraints. Environ Dev Econ 2:88-93.

Naeem S, LJ Thompson, SP Lawlor, JH Lawton and RM Woodfin. 1994. Declining biodiversity can alter the performance of ecosystems. Nature 386:737.

Natural Resources Management Centre. 1980. Mangrove inventory of the Philippines using LANDSAT data. Bakawan 1(1).

Naylor RL, RJ Goldburg, H Mooney, M Beveridge, J Clay, C Folke, N Kautsky, J Lubchenco, J Primavera and M Williams. 1998. Nature's subsidies to shrimp and salmon farming. Science 282:883-884.

Nelson RR. 1995. Recent evolutionary theorizing about economic change. J Econ L 33:48-90.

Nes EH van and M Scheffer. 2005. Implications of spatial heterogeneity for catastrophic regime shifts in ecosystems. Ecology 86:1797-1807.

Neutel A-M. 2001. Stability of Complex Food Webs: Pyramids of Biomass, Interaction Strengths and the Weight of Trophic loops. PhD Dissertation, University of Utrecht.

Neutel A-M, JP Heesterbeek and PC de Ruiter. 2002. Stability in real food webs: weak links in long loops. Science 296:1120-1123.

Newman MEJ. 2000. Models of the small world. J Stat Phys 101:819-841.

Ney-Nifle M and M Mangel. 2000. Habitat Loss and Changes in the Species-Area Relationship. Conserv Biol 14:893-898.

Nixon SW. 1995. Coastal marine eutrophication: A definition, social causes and future concerns. Ophelia 41:199-219.

Noailly J. 2003. Coevolutionary Modelling for Sustainable Economic Development. PhD thesis, Free University, Tinbergen Institute and Thesis Publishers, Amsterdam.

Norberg J. 1999. Linking Nature's services to ecosystems: some general ecological concepts. Ecol Econ 29:183-202.

Norgaard RB. 1984. Coevolutionary development potential. Land Econ 60:160-173.

Norgaard RB. 1994. Development betrayed: the end of progress and a coevolutionary revisioning of the future. Routledge, London and New York.

Norgaard RB. 2005. Bubbles in a back eddy: A commentary on the origin, diagnostic attributes and practical application of coevolutionary theory. Ecol Econ 54:362– 365.

Novacek MJ and EE Cleland. 2001. The current biodiversity extinction event: Scenarios for mitigation and recovery. Proc Natl Acad Sc. USA 98:5466-5470.

Odum EP. 1971. Fundamentals of Ecology. Saunders, Philadelphia, PA.

Oliveira SM di, D Alves and JSS Martins. 2000. Evolution and ageing. Physica A 285:77-100.

Ong PS, LE Arfuang, RG and Rosell-Amball (eds) 2002. Philippine biodiversity conservation priorities: a second iteration of the National Biodiversity Strategy and Action Plan. Department of Environment and Natural Resources, Conservation International Philippines, University of the Philippines Center for Integrative and Development Studies and Foundation for the Philippine Environment, Quezon City, Philippines.

Opschoor JB. 1997. Industrial metabolism, economic growth and institutional change. In: M Redclift and G Woodgate (eds). The International Handbook of Environmental Sociology. Edward Elgar, Cheltenham, p 274-287.

Owens IPF and PM Benneth. 2000. Ecological basis of extinction risk in birds: habitat loss versus human persecution and introduced predators. Proc Natl Acad Sc. USA 97:12144-12148.

Pace M, JJ Cole, SR Carpenter and JF Kitchell. 1999. Trophic cascades revealed in diverse ecosystems. Trends Ecol Evol 14:483-488.

Padilla JE and M Tanael. 1997. Assessment of milkfish and prawn culture in brackish water ponds. In: R Janssen and JE Padilla (eds) Mangroves or fishponds? Valuation and evaluation of management alternatives for the Pagbilao mangrove forest. Resources, Environment and

Economics Centre for Studies Inc, Pasig City, Philippines and Institute for Environmental Studies (IVM), Vrije Universiteit, Amsterdam, The Netherlands.

Paez-Osuna F. 2001. The environmental impact of shrimp aquaculture: causes, effects and mitigating alternatives. Environ Manage 28:131-140.

Paine RT. 1969. A note on trophic complexity and species diversity. Am Nat 103:91–93

Paine RT. 1988. Food webs: road maps of interactions or grist for theoretical development? Ecology 69:1648-1654.

Paine RT. 1992. Food web analysis through field measurement of per capita interaction strength. Nature 355:73-75.

Palumbi SR. 2001. Humans as the World's Greatest Evolutionary Force. Science 293:1786-1790.

Parker IM, D Simberloff, WM Lonsdale, K Goodell, M Wonham, PM Kareiva, MH Williamson, B van Holle, PB Moyle, JE Byers and L Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. Biol Inv 1:3-19.

Parker MA. 1999. Mutualism in metapopulations of legumes and rhizobia. Am Nat 153 Supplement:S48-S60.

Parmesan C and G Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37-42.

Pauly D, V Christensen, J Dalsgaard, R Froese and F Torres F Jr. 1998. Fishing down marine food webs. Science 279:860-863.

Pellmyr O and CJ Huth. 1994. Evolutionary stability of mutualism between yuccas and yucca moths. Nature 372:257-260.

Penn DJ. 2003. The evolutionary roots of our environmental problems: towards a Darwinian ecology. Q Rev Biol 78: 275-301.

Petchey OL and KJ Gaston. 2002. Functional diversity (FD), species richness and community composition. Ecol Lett 5:402-411.

Petchey OL, PT McPhearson, TM Casey and PJ Morin. 1999. Environmental warming alters food-web structure and ecosystem function. Nature 402:69–72.

Peterson G. 2003. Political ecology and ecological resilience: an integration of human and ecological dynamics. Ecol Econ 35:323-336.

Peterson G, CR Allen and CS Holling. 1998. Ecological resilience, biodiversity and scale. Ecosystems 1:6-18.

Pierce NE. 1984. Amplified species diversity: a case study of an Australian Lycaenid butterfly and its attendant ants. In: RI Vane-Wright and PR Ackery (eds) Biology of Butterflies. XI Symposium of the Royal Entomological Society of London. Academic Press, London, p 197-200.

Pierce NE, RL Kitching, RC Buckley, MFJ Taylor and KF Kenbow. 1987. The costs and benefits of cooperation between the Australian lycaenid butterfly *Jalmenus evagoras* and its attendant ants. Behavioural Ecology and Sociobiology 21:237-248.

Pimentel D, L Lach, R Zuniga and D Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. Bioscience 50:53-65.

Pimm SL. 1982. Food Webs. Chapman Hall, London.

Pimm SL. 1984. The complexity and stability of ecosystems. Nature 307:321-326.

Pimm SL. 1998. Extinction. In: WJ Sutherland (ed) Conservation Science and Action. Blackwell Science, Oxford, p 20-38.

Pimm SL and RA Askins. 1995. Forest losses predict bird extinctions in eastern North America. Proc Natl Acad Sc. USA 92:9343-9347.

Pimm SL, HL Jones and J Diamond J. 1988. On the risk of extinction. Am Nat 132:757-785.

Pimm SL and JH Lawton. 1978. Number of trophic levels in ecological communities. Nature 275:542-544.

Pimm SL and JH Lawton. 1980. Are food webs divided into compartments? J Ani Ecol 49:879-898.

Pimm SL, GJ Russel, JL Gittleman and TM Brooks. 1995. The future of biodiversity. Science 269:347-350.

Piraino S, G Fanelli and F Boero. 2002. Variability of species' roles in marine communities: change of paradigms for conservation priorities. Mar Biol 140:1067-1074.

Polis GA and DR Strong,.1996. Food web complexity and community dynamics. Am Nat 147:813-846.

Polis GA, ALW Sears, GR Huxel, DR Strong and J Maron. 2000. When is a trophic cascade a trophic cascade? Trends Ecol Evol 15:473-475.

Power ME, D Tilman, JA Estes, BA Menge, WJ Bond, LS Mills, D Gretchen, JC Castilla, J Lubchenco and RT Paine. 1996. Challenges in the quest for keystones. Bioscience 46:609–620.

Pratchett T. 1997. Jingo. Victor Gollancz Ltd, London.

Pratchett T. 1998. The Last Continent. Corgi Books, London.

Pratchett T. 2003. Monstrous Regiment. HarperCollins Publishers Inc, New York.

Pratchett T. 2005. Going Postal. Corgi Books, London.

Price EO. 1999. Behavioral development in animals undergoing domestication. Appl Anim Behav Sci 65:245-271.

Prigogine I. 1984. Order Out of Chaos. Bantam New Age.

Prigogine I and I Stengers. 1985. Order Out of Chaos: Man's new dialogue with nature. Fontana Paperbacks, London.

Primavera JH. 1998. Mangroves as Nurseries: Shrimp Populations in Mangrove and Non-mangrove Habitats. Estuar Coast Shelf S 46:457-464.

Proctor H and I Owens. 2000. Mites and birds: diversity, parasitism and coevolution. Trends Ecol Evol 15:358-364.

Purvis A, JL Gittleman, G Cowlishaw and GM Mace. 2000. Predicting extinction risk in declining species. Proc R Soc Lond B Bio 267:1947–1952.

Raan AFJ van. 1990. Fractal dimension of co-citations. Nature 347:626.

Rahmstorf S. 1999. Shifting seas in the greenhouse? Nature 399:523-524.

Rammel C and M Staudinger. 2002. Evolution, variability and sustainable development. Int J Sust Dev World 9:301–315.

Rammel C and Bergh JCJM van den. 2003. Evolutionary policies for sustainable development: Adaptive flexibility and risk minimising. Ecol Econ 47:121– 133.

Raup D. 1993. Extinctions: Bad Genes or Bad Luck? Oxford University Press, Oxford.

Ravasz E, AL Somera, DA Mongru, ZN Oltvai and A-L Barabási. 2002. Hierarchical organization of modularity in metabolic networks. Science 297:1551-1555.

Redman CL, JM Grove and LH Kuby. 2004. Integrating social science into the Long-Term Ecological Research (LTER) Network: Social dimensions of ecological change and ecological dimensions of social change. Ecosystems 7: 161–171

Redner S. 1998. How popular is your paper? An empirical study of the citation distribution. Eur Phys 4:131-134.

Ridley M. 1996. Evolution. 2nd edition. Oxford Press, Oxford.

Rietkerk M, SC Dekker, PC de Ruiter and J van Koppel. 2004. Self-organized patchiness and catastrophic shifts in ecosystems. Science 305:1926-1929.

Riley A. 2005. Return of the Bunny Suicides. Penguin Books, London.

Ritchie ME and Holff. 1999. Spatial scaling laws yield a synthetic theory of biodiversity. Nature 400:557-560.

Rodionov S and JE Overland. 2005. Application of a sequential regime shift detection method to the Bering Sea ecosystem. ICES J Mar Sc 62:328-332.

Root TL, JT Price, KR Hall, SH Schneider, C Rosenzweig and A Pounds. 2003. Fingerprints of global warming on wild animals and plants. Nature 421:57-60.

Rosenzweig ML. 1995. Species Diversity in Space and Time, Cambridge University Press, Cambridge, UK.

Rosenzweig ML. 2001. Loss of speciation rate will impoverish future diversity. Proc Natl Acad Sc. USA 98:5404-5410.

Roy K, JW Valentine, D Jablonski and SM Kidwell. 1996. Scales of climatic variability and time averaging in Pleistocene biotas: implications for ecology and evolution. Trends Ecol Evol 11:458-463.

Ruiter PC de, A-M Neutel and JC Moore. 1995. Energetics, patterns of interaction strengths and stability in real ecosystems. Science 269:1257-1260.

Salomons W. 2004. European Catchments: catchment changes and their impact on the coast. Report R-04/01, Institute for Environmental Studies, Vrije Universiteit, Amsterdam, the Netherlands.

Scheffer M and J Beets. 1994. Ecological models and the pitfalls of causality. Hydrobiologia 276:115-124.

Scheffer M and SR Carpenter. 2003. Catastrophic regime shifts in ecosystems: linking theory to observation. Trends Ecol Evol 18:648-656.

Scheffer M, SR Carpenter, JA Foley, C Folke and B Walker. 2001. Catastrophic shifts in ecosystems. Nature 413:591–596.

Schlaepfer MA, MC Runge and PW Sherman. 2002. Ecological and evolutionary traps. Trends Ecol Evol 17:474-480.

Schlager W. 1999. Scaling of sedimentation rates and drowning of reefs and carbonate platforms. Geology 183-186.

Schluter, D. 2000. Ecological Character Displacement in Adaptive Radiation. Am Nat 156 Supplement:S4-S16.

Schluter D. 2001. Ecology and the origin of species. Trends Ecol Evol 16:372-380.

Schmid B. J Joshi and F Schläpfer. 2002. Empirical evidence for biodiversity–ecosystem functioning relationships. In: AP Kinzig, SW Pacala, D Tilman (eds). Functional Consequences of Biodiversity: Experimental Progress and Theoretical Extensions Princeton University Press, Princeton.

Schmitz O, PA Hambäck and AP Beckerman. 2000. Trophic Cascades in Terrestrial Systems: A Review of the Effects of Carnivore Removals on Plants. Am Nat 155:141.

Schoener TW. 1989. Food webs from the small to the large: Ecology 70:1559-1689.

Schön D. 1983. The Reflective Practitioner: how professionals think in action. Basic Books, New York.

Schumpeter JA. 1964. Business Cycles: A Theoretical, Historical and Statistical Analysis of the Capitalist Process. McGraw-Hill, New York, NY.

Scott DA and CM Poole. 1989. A Status Overview of Asian Wetlands. Kuala Lumpur, Malaysia. Asian Wetlands Bureau Report No 53, Kuala Lumpur, Malaysia.

Seglen PO. 1992. The skewness of science. J Am Soc Inf Sci 43:628-638.

Selden T and D Song. 1994. Environmental quality and development: is there a Kuznets curve for air pollution emissions? J Environ Econ Manag 27:147-162.

Senge PM. 1994. The Fifth Discipline: the Art and Practice of the Learning Oorganization. Currency Doubleday, New York.

Sethi R and E Somanathan. 1996. The evolution of social norms in common property resource use. Am Econ Rev 86: 766-788.

Sheridan P. 1997. Benthos of adjacent mangrove, seagrass and non-vegetated habitats in Rookery Bay, Florida, USA. Estuar Coast Shelf S 44:455-469.

Simberloff D. 1998. Flagships, umbrellas and keystones: is single-species management passe in the landscape era? Biol Cons 83:247–257.

Smith JM. 1989. The causes of extinction. Philos Trans R Soc Lond B 325:241-252.

Sober E and DS Wilson. 1998. Unto Others: The Evolution and Psychology of Unselfish Behavior. Harvard University Press, Cambridge, Massachusetts.

Solé RV. 2000. Modelling Macroevolutionary Patterns: An Ecological Perspective. Santa Fe Institute Working Paper No. 00-12-063.

Solé RV, D Alonso and A McKane. 2002. Self-organized instability in complex ecosystems. Phil Trans R Soc Lond B 357:667-681.

Solé RV and JM Montoya. 2001. Complexity and fragility in ecological networks. Proc R Soc Lond B Bio 268:2039-2045.

Soule ME (ed) 1987. Viable Populations for Conservation, Cambridge University Press, Cambridge, UK.

Stachowicz J. 1999. Species diversity and invasion resistance in a marine ecosystem. Science 286:1577-1579.

Stauffer D and N Jan. 1994. Size effects in Kauffman-type evolution for rugged fitness landscapes. J Theor Biol 168:211-218.

Stearns SC and RF Hoekstra. 2000. Evolution: an introduction. Oxford University Press, Oxford.

Steel RGD and JH Torrie. 1981. Principles and Procedures of Statistics: A Biometrical Approach. 2nd edition. McGraw-Hill Book Company, London.

Stevens L, CJ Goodnight and S Kalisz. 1995. Multi-level selection in natural populations of *Impatiens capensis.* Am Nat 145:526.

Stowe KA, RJ Marquis, CG Hochwender and EL Simms. 2000. The evolutionary ecology of tolerance to consumer damage. Ann Rev Ecolog Syst 31:565-595.

Straalen NM van and MJTN Timmermans. 2002. Genetic variation in toxicant-stressed populations: an evaluation of the "genetic erosion" hypothesis. Hum Ecol Risk Assess 9:983-1002.

Stirling I and WR Archibald. 1977. Aspects of predation of seals by polar bears. J Fish Res Board Can 34**:**1126-1129.

Strauss SY and AA Agrawal. 1999. The ecology and evolution of plant tolerance to herbivory. Trends Ecol Evol 14:179-185.

Strickberger MW. 1996. Evolution. Second edition. Jones and Bartlett Publishers, Sudbury, Massachusetts.

Strogatz SH. 2001. Exploring complex networks. Nature 410:268-276.

Strong DR 1992. Are trophic cascades all wet? Differentiation and donor-control in speciose ecosystems. Ecology 73:747–754.

Sutherland WJ, S Armstrong-Brown, PR Armsworth, T Brereton, J Brickland, CD Campbell, DE Chamberlain, AI Cooke, NK Dulvy, NR Dusic, M Fitton, RP Freckleton, H CJ Godfray, N Grout, HJ Harvey, C Hedley, JJ Hopkins, NB Kift, J Kirby, WE Kunin, DW Macdonald, B Marker, M Naura, AR Neale, T Oliver, D Osborn, AS Pullin, MEA Shardlow, DA Showler, PL Smith, RJ Smithers, J-L Solandt, J Spencer, CJ Spray, CD Thomas, J Thompson, SE Webb, DW Yalden and AR Watkinson. 2006. The identification of 100 ecological questions of high policy relevance in the UK. J Appl Ecol 43: 617–627.

Svirezhev YM and A Svirejeva-Hopkins. 1998. Sustainable biosphere: critical overview of basic concept of sustainability. Ecol Model 106:47-61.

Swenson W, DS Wilson and R Elias. 2000. Artificial ecosystem selection. Proc Natl Acad Sc. USA 97:9110-9114.

Tegner MJ and PK Dayton. 1999. Ecosystem effects of fishing. Trends Ecol Evol 14:261-262.

Templeton AR, RJ Robertson, J Brisson and J Strasburg. 2001. Disrupting evolutionary processes: The effect of habitat fragmentation on collared lizards in the Missouri Ozarks. Proc Natl Acad Sc. USA 98:5426-5432.

The IUCN Species Survival Commission. 2004. IUCN Red List of Threatened Species. IUCN, http://www.iucnredlist.org/.

Thimdee W, G Deein, C Sangrungruang and K Matsunaga. 2004. Analysis of primary food sources and trophic relationships of aquatic animals in a mangrove-fringed estuary, Khung Krabaen Bay (Thailand) using dual stable isotope techniques. Wetlands Ecology and Management 12:135-144.

Thomas F, R Poulin, J-F Guégan, Y Michalakis and F Renaud. 2000. Are there pros as well as cons to being parasitized? Parasitol Today 16:533-536.

Thompson JN. 1994. The Coevolutionary Process. University of Chicago Press, Chicago.

Thompson JN. 1999a. Coevolution and Escalation: Are ongoing coevolutionary meanderings important? Am Nat 153 Supplement:S92-S93.

Thompson JN. 1999b. Specific hypotheses on the geographic mosaic of coevolution. Am Nat 153 Supplement:S1-S14.

Thompson JN. 1999c. The evolution of species interactions. Science 284:2116-2118.

Thompson JN and BM Cunningham. 2002. Geographic structure and dynamics of coevolutionary selection. Nature 417:735-738.

Tilman D and JA Downing. 1994. Biodiversity and stability in grasslands. Nature 367:363-365.

Tilman D, J Knops, D Wedin and P Reich. 2002. Plant diversity and composition: effects on productivity and nutrient dynamics of experimental grasslands. In: M Loreau, S Naeem and P Inchausti (eds) Biodiversity and Ecosystem Functioning. Oxford Univ. Press, Oxford, p 21–35.

Tilman D and C Lehman. 2001. Human-caused environmental change: Impacts on plant diversity and evolution. Proc Natl Acad Sc. USA 98:5433-5440.

Tilman D, R May, C Lehman and M Nowak. 1994. Habitat destruction and extinction debt. Nature 371:65-66.

Timmerman A, J Oberhuber, A Bacher, M Esch, M Latif and E Roeckner. 1999. Increased El Niño frequency in a climate model forced by future greenhouse warming. Nature 398:694-696.

Tisdell C. 2001. Globalisation and sustainability: environmental Kuznets curve and the WTO. Ecol Econ 39:185-196.

Tong AHY, G Lesage, GD Bader, H Ding, H Xu and X Xin. 2004. Global mapping of the yeast genetic interaction network. Science 303:808-813.

Towns DR, CH Daugherty and A Cree. 2001. Raising the prospects for a forgotten fauna: a review of 10 years of conservation effort for New Zealand reptiles. Biol Cons 99:3-16.

Tributsch H, H Goslowsky, U Küppers and H Wetzel. 1990. Light collection and solar sensing through the polar bear pelt. Sol Energ Mater 21:219-236.

Trivers RL. 1971. The evolution of reciprocal altruism. Q Rev Biol 46:35-57.

Turner RK, I Lorenzoni, N Beumont, IJ Bateman, IH Langford and AL McDonald. 1998. Coastal management for sustainable development: Analysing environmental and socio-economic changes on the UK coast. Geogr J 164:269-281.

Ullrich SM, TW Tanton and SA Abdarshitova. 2001. Mercury in the aquatic environment: a review of factors affecting methylation. Environ Sci Technol 31:241-293.

UN (United Nations), 1993. Input-output tables and analysis. New York.

UNEP-WCMC. 2006. In the front line: shoreline protection and other ecosystem services from mangroves and coral reefs. UNEP-WCMC, Cambridge, UK, 33 pp.

Van Valen LM. 1973. A new evolutionary law. Evol Theor 1:1-30.

Veeren RJHM van der and CM Lorenz. 2002. Integrated economic–ecological analysis and evaluation of management strategies on nutrient abatement in the Rhine basin. J Environ Manage 66:361-376.

Vellinga P and N Herb. 1999. Industrial Transformation Project: IT Science Plan. IHDP Report No 12, Bonn, Germany.

Vermaat JE, RN Rollona, CDA Lacap, C Billot, F Alberto, HME Nacorda, F Wiegman, J Terrados. 2004. Meadow fragmentation and reproductive output of the SE Asian seagrass *Enhalus acoroides*. J S Res 52:321– 328.

Vitousek PM, CM D'Antonio, LL Loope, M Rejmanek and R Westbrooks. 1997a. Introduced species: A significant component of human-caused global change. N Z J Ecol 21:1-16.

Vitousek PM, JD Aber, RW Howarth, GE Likens, PA Matson, DW Schindler, WH Schlesinger and DG Tilman. 1997a. Human alteration of the global nitrogen cycle: Sources and consequences. Ecol Appl 7:737-750.

Vitousek PM, PR Ehrlich, AH Ehrlich and PA Matson. 1986. Human appropriation of the products of photosynthesis. Bioscience 36:368-373.

Waldrop WM. 1992. Complexity. Simon and Schuster, New York.

Wallace R and RG Wallace. 1998. Information Theory, Scaling Laws and the Thermodynamics of Evolution. J Theor Biol 192: 545-559.

Walters C. 1986. Adaptive Management of Renewable Resources. Macmillan, New York.

Walters C. 1997. Challenges in adaptive management of riparian and coastal ecosystems. Conservation Ecology 1(2):1. http://www. consecol. org/vol1/iss2/art1/.

Walther G-R, E Post, P Convey, A Menzel, C Parmesan, TJC Beebee, J-M Fromentin, O Hoegh-Guldberg and F Bairlein. 2002. Ecological responses to recent climate change. Nature 416:389-295.

Ward SA and IWB Thornton. 1998. Equilibrium theory and alternative stable equilibria. J Biogeog 25:615-622.

Wasserman S and K Faust. 1994. Social Network Analysis. Cambridge Univ. Press, Cambridge, UK.

Watts DJ. 1999. Small Worlds: The Dynamics of Networks Between Order and Randomness. Princeton University Press, Princeton, NJ.

Watts DJ and SH Strogatz. 1998. Collective dynamics of 'small-world' networks. Nature 393:440-442.

Webb T and PJ Bartlein. 1992. Global changes during the last 3 million years - climatic controls and biotic responses. Ann Rev Ecolog Syst 23:141-173.

Weeks P. 2000. Red-billed oxpeckers: vampires or tickbirds? Behav Ecol 11:154-160.

Western D. 2001. Human-modified ecosystems and future evolution. Proc Natl Acad Sc. USA 98:5458-5465.

Wikel SK and D Bergman. 1997. Tick-host immunology: significant advances and challenging opportunities. Parasitol Today 13:383-389.

Wilkinson C. 2000. Status of coral reefs of the world: 2000. Australian Institute of Marine Science, Townsville. 363pp.

Williams RJ, EL Berlow, JA Dunne, A-L Barabási and ND Martinez. 2002. Two degrees of separation in complex food webs. Proc Natl Acad Sc. USA 99:12913-12916.

Williams RJ. and ND Martinez. 2000. Simple rules yield complex food webs. Nature 404:180-183.

Williamson MH. 1996. Biological Invasions. Chapman and Hall, London.

Wilson DS and E Sober. 1994. Reintroducing group selection to the human behavioral sciences. Behav Brain Sci 17:585-608.

Winder N, BS McIntosh and P Jeffrey. 2005. The origin, diagnostic attributes and practical application of co-evolutionary theory. Ecol Econ 54: 347-361.

With KA and TO Crist. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76:2446-2459.

Witt U. 1997. Self-organisation and economics - what is new? Struct Change Econ Dynam 8:489-507.

Witte R, T Goldschmide, J Wanink, M van Oijen, K Goudswaard, E Witte-Mass and N Boulton. 1992. The destruction of an endemic species flock: quantitative data on the decline of haplochromine cichlids of Lake Victoria. Environ Biol Fishes 34:1-28.

Wood RA, AB Keen, JFB Mitchell and JM Gregory. 1999. Changing spatial structure of the thermohaline circulation in response to atmospheric CO2 forcing in a climate model. Nature 399:572-575.

Woodruff DS. 2001. Declines of biomes and biotas and the future of evolution. Proc Natl Acad Sc. USA 98:5471-5476.

Wright S. 1968. Evolution and Genetics of Populations. Vol 1: Genetic and biometric foundations, University of Chicago Press, Chicago.

Wright S. 1977. Evolution and Genetics of Populations. Vol 3: Experimental results and evolutionary deductions, University of Chicago Press, Chicago.

Wu J and D Marceau. 2002. Modeling complex ecological systems: an introduction. Ecol Model 1553:1-6.

Wu J and JL David. 2002. A spatially explicit hierarchical approach to modeling complex ecological systems: theory and applications. Ecol Model 153:7-26.

Wu D, SC Daugherty, SE van Aken, GH Pai, KL Watkins, H Khouri1, LJ Tallon, JM Zaborsky, HE Dunbar, PL Tran, NA Moran and JA Eisen. 2006. Metabolic complementarity and genomics of the dual bacterial symbiosis of sharpshooters. PLOS Biology 4:1079-1092.

Yodzis P. 1981. The stability of real ecosystems. Nature 289:674-676.

Yu DW. 2001. Parasites of mutualisms. Biol J Linn Soc 72:529-546.

Yu DW and NE Pierce. 1998. A castration parasite of an ant-plant mutualism. Proc R Soc Lond B 265:375-382.

Glossary

Adaptation 1) Acclimatisation
2) Feature of an organism enabling it to survive and reproduce in its natural environment better than if it lacked the feature.
3) A character that continues to serve the function for which it originally evolved (see Exaptation).
4) The process by which organisms become adapted.
5) Adjustment in natural or human systems in response to actual or expected climatic stimuli or their effects, which moderates harm or exploits beneficial opportunities.

Adaptive cycle A metaphor used to describe four commonly occurring phases of change in complex systems. The four phases are: exploitation, conservation, creative destruction, and renewal (also referred to as r, K, omega, alpha).

Adaptive landscape Graph of the average fitness of a population in relation to the frequencies of genotypes in it: a peak on the landscape corresponds to genotypic frequencies at which the average fitness is high; valleys correspond to genotypic frequencies at which average fitness is low.

Adaptive management A systematic process for continually improving management policies and practices by learning from the outcomes of operational programs.

Adaptive trait Any phenotypic trait that confers reproductive advantage on the individual possessing it.

Allele One of two or more forms of a gene.

Allopatry Species occur in different geographical regions or are separated by a spatial barrier (see Sympatry).

Altruism Sacrifice, even self-destructive behaviour, benefiting others.

Amensalism Species interaction where one species is inhibited (incurs costs) and the other unaffected. Common examples are when one organism exudes a chemical compound, as part of its normal metabolism, that is detrimental to another organism.

Antagonism An interaction which engenders a cost on at least one participant (see Consumption, Amensalism and Competition).

Aquaculture The controlled cultivation and harvest of aquatic plants or animals. Intensive, semi-intensive and extensive aquaculture may be distinguished on the basis of stocking rates and the use of artificial feeds and chemicals.

Assemblage A collection of plants and/or animals characteristically associated with a particular environment that can be used as an indicator of that environment.

Attractor Interplay between feedback processes generates macro patterns termed bounded stability. These patterns are similar to the chaotic or strange at-tractors of chaos theory (see Stability).

Autotroph An organism that uses carbon dioxide as its main or sole source of carbon. Usually a plant. Also termed producer (see Heterotroph).

Basal species In food webs, species with predators but no prey.

Benefit See Fitness benefit.

Bifurcation Abrupt and often dramatic qualitative changes in the overall behaviour pattern of a complex adaptive system.

Biodisparity Morphological and physiological variability.

Biogeographical province Biological subdivision of the Earth's surface on the basis of taxonomic rather than ecological criteria, and embracing both faunal and floral characteristics.

Biodiversity A shortening of 'biological diversity'. The variety of life in terms of genetic diversity, species diversity, and ecological diversity.

Biotic exchange Human-mediated introduction of species.

Broad-scale degree distribution See Truncated power law degree distribution.

By-product benefit Benefits which accrue to an individual as a result of the selfish behaviour of another.

Carnivory Feeding on flesh by a heterotroph (see Herbivore, Heterotroph, Autotroph).

Character Any recognisable trait, feature or property of an organism.

Character displacement Divergence in competing species. An evolutionary process that accentuates differences between closely related species which are sympatric. The characters involved can be morphological, ecological, behavioural, or physiological, and it is assumed that they are genetically based (see Sympatry, Allopatry, Competition).

Characteristic path length Number of edges or links in the shortest path between two nodes, averaged over all pairs of nodes (see Node, Complex network).

Cheating Any behaviour that extracts, with minimal or no reciprocation, a benefit that is normally exchanged in a cooperative interaction, thereby reducing the fitness of one of both cooperating partners.

Clustering Tendency of groups of nodes to be connected to each other (see Node, Complex network).

Coevolution 1) Reciprocal evolutionary change between interacting species.

2) Mutual or reciprocal causality between components of a complex adaptive system.

Commensalism Species interaction in which one derives benefits without affecting the other.

Commodities Goods and services produced by economy.

Compensation Derivation of benefits from consumption to compensate for its costs (see Consumption-1).

Competition Interaction among individuals striving for the same thing. Both parties suffer costs. Competition may be intraspecific (among individuals of the same species) or interspecific (among individuals of different species).

Complex adaptive system System composed of a heterogeneous assemblage of types, in which structure and function emerge from the balance between the constant production of diversity, due to various forces, and the winnowing of that diversity through a selection process mediated by local interactions.

Complex network Model describing the interactions among components of complex systems. Also termed disordered networks (see also Node, Regular lattice, Random graph).

Congeners Very closely related species (sister taxa) that are incompletely, or only recently completely, reproductively isolated from one another.

Connectance Proportion of all possible interactions (links) among the components of a system (nodes of a network) that are realised (see Link, Node, Complex network, Directed connectance, Interactive connectance).

Consumption 1) In ecology, a species interaction in which one species uses another species as a source of food. The consumer enjoys a positive effect from resources gained; the consumed suffers a negative effect from resources lost (see Herbivore, Victim, Parasite, Host, Predator, Prey).
2) In economics consumption is defined in terms of the use of goods and services. It is equated with the total expenditure in an economy on goods and services used up within a specified period of time (usually a year). This expenditure not only includes goods and services, but also the raw materials, labour etc. used in production processes.

Cooperation 1) Usually restricted to intraspecific interactions where there is mutual benefit.

2) In this dissertation, an evolutionary process which promotes benefits to competitors facing a common problem (see Competition).

Cost See Fitness cost.

Criticality See Self-organised criticality.

Degree distribution Frequency distribution of links among nodes (see Node, Link, Scale-free).

Deme Reproductively isolated sub-population (see Trait-group selection).

Detritivore Heterotrophic organism that feeds on dead material (or detritus).

Dinoflagellates An order of heterotrophic protozoans closely allied with brown algae and diatoms. They are sometimes classified as algae.

Directed connectance Measure of connectance which includes the direction of interaction, and so the possibility of mutual interaction (*a* eats *b* while *b* eats *a*) and self-interaction or cannibalism (*a* eats *a*) (see Connectance).

Diversity Species richness of a community or area (see Species Richness).

Down-sizing Mean body size of species in communities subject to social predation diminishes.

Ecological niche The functional position of an organism in its environment, comprising the habitat in which the organism lives, the periods of time during which it occurs and is active there, and the resources it obtains there (see Ecospace).

Ecological redundancy Multiple species available to fill a functional role.

Ecological resilience According to some authors, the same as the second definition of resilience (see Resilience, Engineering resilience).

Ecological trap When an organism makes a maladaptive habitat choice because recent anthropogenic change in the environment has broken the normal cue-habitat quality correlation (see Evolutionary trap).

Ecospace The sum of all available niches (see Ecological niche)

Edge effects Negative effects on species and ecological processes caused by the increase in the amount of habitat edge as a result of habitat fragmentation.

Ecosystem engineer An organism that directly or indirectly modulates the availability of resources to other species by causing physical state changes in biotic or abiotic materials

El Niño-Southern Oscillation Oceanographic and meteorological event leading to a plume of nutrient-poor, warm water that pushes down the western coast of South America.

Emergence Over-all pattern, structure or organisation of a complex adaptive system that it is not simply an aggregation of individual actions, but has unique properties not possessed by the individuals alone.

Engineering resilience According to some authors, the equivalent of equilibrium resilience (see Resilience-1, Equilibrium resilience)

Engineering network Networks of species which rely on one another for habitat (see Food web, Niche construction)..

Environmental Kusnet's U-curve Postulates that environmental clean-up follows wealth creation.

Epiphyte A plant that grows upon another plant, but is neither parasitic on it nor rooted in the ground.

Epistasis	The situation in which an allele of one gene (the epistatic gene) prevents the expression of all allelic alternatives of another gene.
Equilibrium	A state of dynamic systems in which there is no net change.
Equilibrium resilience	Measure of stability that assumes system stability increases as time required to return to equilibrium decreases after a perturbation.
Equilibrium stability	Discrete measure that considers a system stable if it returns to its equilibrium after a small perturbation away from the equilibrium (see Equilibrium, General Stability).
Escalation	An increase to counteract a perceived discrepancy.
Evolution	Descent with modification. Change in a lineage of populations between generations (see Lineage)
Evolutionary arms race	Thwarting of adaptations by another (see Escalation).
Evolutionary trap	When an organism makes a maladaptive choice because recent anthropogenic change in the environment has broken the normal link between environmental cue and behavioural and life-history decisions, such as when to migrate, when to reproduce, and what to eat (see Ecological trap).
Exaptation	A trait that arose for one purpose but that came to fulfil a different adaptive purpose (see Adaptation-3).
Exergy	That part of energy that can be transformed into work.
Extinction	A species becomes extinct if it is unable to evolve rapidly enough to meet changing circumstances, and/or if its niche disappears so that no capacity for rapid evolution could have saved it.
Facultative	Facultative mutualists are capable of living independently of each other (see Mutualism, Obligate).
Feedback mechanism	A control device in a system (see Positive feedback, Negative feedback).
Fitness	1) In evolutionary biology, average number of offspring produced by individuals with a certain genotype, relative to the number produced by individuals with other genotypes. 2) In the study of complex systems, an assumed property of a system that determines the probability that that system will be selected, i.e. that it will survive, reproduce or be produced
Fitness benefit	Positive effect from an interaction which enhances long-term survival.
Fitness cost	Negative effect from an interaction which compromises long-term survival.
Food web	Diagram documenting trophic (feeding) relationships of organisms within an ecological community.
Founder effect	Loss of genetic variation when a new colony is formed by a very small number of individuals from a larger population.
Fractal	A self-similar structure whose geometrical and topographical features are recapitulated in miniature on finer and finer scales.

Fragility Converse of Robustness.

Fragmentation Breakdown of the web of interactions among the nodes of a complex network. The network splits into sub-networks and, in the process, may trigger a cascade of node loss (see Node, Complex network, Robustness, Fragility).

Functional group Collection of organisms based on criteria such as morphological, physiological, behavioural, biochemical, or environmental responses or on trophic criteria.

Gene flow Movement of genes into, or through, a population by interbreeding or by migration and interbreeding. Gene flow occurs because individuals move among populations, mixing genes.

General resilience Measure of stability that assumes system stability increases as return time to the equilibrium-non-equilibrium solution decreases after a per-turbation (see Resilience, Equilibrium resilience).

General stability Measure assuming that stability increases as the lower limit of population density moves further away from zero (see Equilibrium stability).

Genetic drift Random changes in gene frequencies in a population over time.

Genotype Genetic constitution of an organism, as opposed to its physical appearance (see Phenotype)

Good A physical object that has value to people and can be sold for a non-negative price in the marketplace.

Grazer Species that move among and feed on two or more individual victims without necessarily killing them prey (see Consumption).

Group selection See Multilevel selection.

Habitat Living place of an organism or community, characterised by its physical or biotic properties.

Hetertroph An organism unable to manufacture its own food and therefore consumes other organisms (see Autotroph).

Herbivory Grazing on plants by heterotrophic species (see Grazer).

Heritability Proportion of variation in a phenotypic character in a population that is due to 1) individual differences in genotypes, or 2) individual genetic differences that will be inherited by offspring.

Hierarchy Stratified autonomy of complex adaptive systems, with hierarchically nested processes linking micro and macro levels in a loosely coupled manner.

Host Source of food for parasites (see Parasites).

Hub Highly-connected node of a complex network (see Node, Complex network).

Industry Organisational units of the economy that undertake production.

Input-output (I-O) table Table which attempts to record all transactions with a given region's economic activities

Insectivory Feeding on insects.

Interactive connectance Measure of connectance which considers only the presence of interaction, and not the direction of that interaction (see Connectance, Directed connectance).

Invasive species Species introduced into a new environment and which comes to degrade human health and wealth, alter the structure and functioning of otherwise undisturbed ecosystems, and/or threaten native biological diversity

Investment Individuals perform costly acts for another in the hope of increasing the probability of receiving benefits in return (see Mutualism).

Iterative Prisoner's Dilemma (IPD) A theoretical game for examining the emergence and persistence of cooperation in a world characterised by non-cooperation.

Iteroparity Breed repeatedly during a lifetime (see Semelparity).

Keystone species Species with impacts on many other species far beyond what might have been expected from its numbers or biomass.

Lineage An ancestor-descendent sequence of populations, cells or genes.

Link Denotes the existence of an interaction between two components or nodes of a network (see Node, Complex network).

Macroevolution Evolution on a grand scale. Events above the species level, such as the origin of vertebrates, or the origin of flight (see Microevolution).

Mass extinction event Irreversible impact on large numbers of species in diverse taxa across the globe and over a short periods.

Meiofauna That part of the microfauna that inhabits macroalgae, rock fissures, and superficial layers of the muddy sea bottom. They are smaller than 1 mm but larger than 0.1 mm.

Metapopulation Group of conspecific populations that exist at the same time but in different places.

Metastable The ability of a non-equilibrium state to persist for a long period of time.

Microfauna The smallest animals in a community, not visible to the naked eye.

Microevolution Evolution of a small scale, such as changes in gene frequencies within a population (see Macroevolution).

Modern syntesis Synthesis of natural selection (Darwin) and Mendelian inheritance. Also known as the evolutionary synthesis or neo-Darwinism.

Multilevel selection Variation in the fitness of an individual due to properties of the group or groups of which it is a member. Group, species, community and ecosystem selection are related terms.

Mutualism Interspecific interactions in which both partners enjoy a net benefit (see also Cooperation, Symbiosis).

Natural selection Process by which the forms of organisms in a population that are best adapted to the environment increase in frequency, relative to less-well adapted forms, over a number of generations.

Negative feedback Feedback mechanism that tends to counterbalance or dampen positive changes and to maintain stability (see Feedback mechanism, Positive feedback).

Network A system of interconnected components.

Neutralism Interaction between species that incurs neither costs nor benefits to either party.

Niche See Ecological niche

Niche construction Modification of environments by the organisms that occupy them.

Node Component of a system when interactions among components are described as a network (see Complex network, Regular lattice, Random graph).

Obligate Obligate mutualists (see Mutualism, Facultative) are heavily specialised on each other, and cannot live independently.

Omnivory Feeding on species in different trophic levels.

Ovivory Feeding on eggs.

Parasite Species which completes an entire stage of development on a single host individual and is likely to cause some decrease in fitness of this host, as least under some ecological conditions (see Consumption).

Parasitoids Parasites of parasites.

Parcelling A strategy for enforcing cooperation. Partitioning benefits from a single interchange into amounts small enough to make cheating unprofitable.

Partitioning Evolutionary process that reduces antagonism between competitors and achieves ecological separation (see Character displacement, Competition).

Partners Individuals are called partners when: it is in their best interest to help each other and, if by doing so, they increase the probability of being together in the future when, for similar reasons, they will continue to help each other.

Path dependence Any outcome is dependent on the historical path taken to it.

Path length See Characteristic path length.

Phenology The study of the periodicity of leafing, flowering and fruiting in plants; these are generally triggered by periodicities in climate.

Phenotype Observable manifestation of a genotype; those observable properties of an organism produced by the genotype in conjunction with the environment (see Genotype).

Phenotypic plasticity Capacity of a phenotype to vary, owing to environmental influences on the genotype (see Phenotype, Genotype).

Phyologeny Tree of life; branching diagram showing ancestral relations among, say, species. Shows for each species which other species it shares its most recent common ancestor.

Piscivory Feeding on fish.

Planktivory Feeding on plankton.

Positive feedback Feedback mechanism which reinforces or amplifies change (see Feedback mechanism, Negative feedback).

Power law Relations of the form: $y = kx^h$ (see Scale-free).

Predator Species which rapidly kill and eat individual prey (see Consumption, Social predation).

Predation matrix Square matrix that captures feeding interactions among the components of a food web. Cell entries of 1 indicate that the component on the row is eaten by the component of the column; cell entries of 0 indicate no feeding interaction.

Preferential attachment Attachment of nodes to a network preferentially to highly connected nodes or hubs (see Node, Complex network).

Prey Source of food for predators (see Predator).

Production 1) In ecology, total mass of organic matter that is manufactured in an ecosystem during a specified period of time.

2) In economics, all goods and services that are intended to be sold at the market or used by a production unit itself, as well as goods and services produced by the government and non-profit organisation with paid employees.

Production unit A process, line, method, activity or technique, or a combination or series thereof, used to produce a product.

Propagule A structure with the capacity to give rise to a new plant, such as a seed.

Random graph Nodes randomly connected to other nodes (see Node, Complex network, regular lattice).

Raptor A bird of prey, such as an eagle or hawk.

Real world network Network mapping the interactions among components of a real-world system. Many such networks are small-world and scale-free (see Complex network, Small-world, Scale-free).

Reciprocal adaptation See Coevolution.

Reciprocity A strategy for cooperation based on reciprocating partner's behaviour during the last interaction.

Red Queen hypothesis See Escalation.

Regular lattice Array comprising nodes connected to a specific number of other nodes according to a specific pattern (see Node, Complex network, Random graph).

Resilience 1) Measure of stability that assumes system stability increases as time required to return to the original state decreases after a perturbation (see Equilibrium resilience, General resilience, Resistance).

2) Magnitude of stress from which the system can recover or the system's specific thresh-olds for absorbing various stresses (see Resistance, Ecological resilience).

Resistance Measure of the degree to which a variable changes after a perturbation (see Resilience).

Robustness The ability of networks to resist fragmentation and secondary loss of nodes (see Node, Complex network, Fragility).

Scale-free	Property attributed to complex networks with a distribution of links among nodes that decays following a power law (see Node, Complex network, Small-world, Degree distribution).
Self-organised criticality	Distribution of fluctuations in complex systems, from many small to a few large, is no coincidence. A system in a critical state will trigger cascades of all magnitudes.
Self-organising holarchic system (SOHO)	A nested constellation of self-organizing dissipative process/structures organized about a particular set of sources of exergy, materials, and information, embedded in a physical environment
Self-similarity	Features of a structure or process which look alike at different scales of space or time. Chaotic systems show self-similarity across time scales; fractal objects show self-similarity across spatial scales.
Semelparity	Breed once during a lifetime (see Iteroparity).
Sensitivity	Embodies the idea that complex adaptive systems are fundamentally non-linear in causation and can generate unpredictable outcomes across space and in time.
Service	An act or a variety of work done for others.
Single-scale degree distribution	Frequency distribution of links among nodes displaying fast-decaying tails (e.g. exponential and Gaussian distributions) (see Degree distribution, Broad-scale degree distribution, Scale-free).
Small-world	Networks displaying local clustering and short path length (see Complex network, Scale-free).
Social predation	Removal of a species precipitately and completely from their natural environments by humans and their activities (see Predator).
Socio-natural interaction	An interaction between a component of a natural system (e.g. an ecosystem) and a component of asocial system (e.g. an economic production unit). Examples include fish and fishers, trees and foresters, charismatic species and conservation groups.
Socio-natural network	A spatially-bounded network of socio-natural interactions.
Specialization	Limitation in the number of other species with which a particular species interacts.
Speciation	Separation of populations of organisms originally able to interbreed, into independent evolutionary units that can interbreed no longer.
Species area Relationship (SAR)	Relationship specifying how the number of species increases as the area of a habitat increases. The SAR can also show how species numbers decline with habitat loss.
Species richness	Total number of species (see also Diversity).
Stabilising selection	Selection tending to keep the form of a population constant. Individuals with mean value for a character have high fitness, while extreme values have low fitness.
Stability	The tendency to return to normative behaviour, such as an equilibrium.
Sustainable development	Development that seeks to meet the needs and aspirations of the present without compromising the ability to meet those of the future.

Sympatry	Species occur in the same area (see Allopatry).
Symbiosis	Definitions vary from intimate mutualisms (see Mutualism), to a synonym for mutualism, to morphologically and physiologically intimate relationships which may or may not benefit both parties.
System	An interacting group of items forming a unified whole.
Taxon (pl. taxa)	Group of organisms of any taxonomic rank such as genus or species.
Top predator	Predator which is not preyed on, and so occupies the highest trophic level of a food web (see Predator, Trophic level, Food web).
Topology	A branch of mathematics that refers to spatial relationships such as adjacency and connectivity.
Trait-group selection	Selection favouring demes with more altruistic alleles. Such demes have a higher fitness that those with fewer altruistic alleles (see Deme).
Trophic cascade	A strong effect imposed by top predators such that it affects, not only the prey population, but also the organisms on which the prey feed, and so on down the food web
Trophic level	A step in the transfer of food and energy within a chain.
Trophic loop	Pathway of interactions from a certain species through the food web back to the same species without visiting other species more than once; a closed chain of trophic links.
Trophic species	Functional groups of taxa that share the same set of predators and prey within a food web.
Truncated power law degree **distribution**	Frequency distribution of links among nodes which displays initially power-law decay followed by a sharp cut-off in the tail (see Degree distribution, Single-scale degree distribution, Scale-free).
Upper connectance	Measure of connectance based on interactive connectance; includes competitive interactions by assuming that, if two predators consume the same prey, they are in competition (see Connectance, Interactive connectance).
Variability	Variance in population densities over time, usually measured as the coefficient in variation.
Vertex	See Node.
Victim	Source of food for grazers (see Grazer).
Vulnerability	Low ecological resilience (see Ecological resilience, resilience).

Samenvatting

Co-evolutie in Complexe Netwerken
een analyse van sociaal-natuurlijke interacties voor 'wetland' beheer

Concepten uit de evolutietheorie duiken de laatste jaren regelmatig op in het milieubeheer. Adaptatie aan klimaatverandering en adaptief beheer zijn hiervan twee voorbeelden. Co-evolutie tussen sociale en natuurlijke systemen, is een ander voorbeeld bestaand uit interactie, wederzijdse dynamiek en wederkerige aanpassing. Dit idee is afgeleid van de evolutiebiologie waar de interactie tussen soorten veel voorbeelden heeft opgeleverd van wederkerige adaptatie. Co-evolutie maakt ook deel uit van het onderzoek naar complexe adaptieve systemen. Het perspectief wordt verbreed van interactie tussen twee soorten naar de interactie tussen de componenten van complexe systemen, en de invloed hiervan op ontwikkelende systeemeigenschappen.

Dit proefschrift richt zich op het vergelijken van verschillende typen van menselijke beïnvloeding van ecosystemen. Het doel van dit proefschrift is:

> *"ontwikkelen van een aanpak voor het beoordelen van effecten van verschillende typen van menselijke beïnvloeding op de toekomstige co-evolutie van elkaar beïnvloedende natuurlijke en sociale systemen."*

Mijn aanpak bestaat uit twee elementen: 1. een methode die het effect van beïnvloeding op co-evolutie simuleert, en 2. een criterium en indicatoren voor het vergelijken van de effecten van verschillende typen beïnvloeding.

Ik noem deze methode topologische netwerkanalyse om mijn focus op de topologie – het aantal en de patroon van de interacties – van complexe netwerken aan te duiden. Topologische analyse verschilt van functionele analyse, omdat functionele analyse niet alleen de structuur maar ook de dynamiek van een netwerk beschrijft, zoals bijvoorbeeld de mate waarin onderdelen materiaal uitwisselen. Een sociaal-natuurlijk netwerk integreert de interacties binnen en tussen een natuurlijk en sociaal systeem. Topologische netwerk analyse bepaalt het effect van menselijke beïnvloeding op de topologie van zo'n netwerk. Mogelijke beïnvloedingen zijn vertaald in risico's voor het uitsterven van soorten. Voor elk alternatief worden zowel het aantal als de soorten die uitsterven als gevolg van menselijke beïnvloeding geïdentificeerd.

Mijn proefschrift omvat drie delen: literatuurstudie, theoretische ontwikkeling en toepassing. De literatuurstudie identificeert elementen voor het generaliseren en operationaliseren van 'co-evolutie' voor milieubeheer. Het levert drie producten op die verder worden uitgewerkt in het tweede deel van het proefschrift:

1. een categorisatie van maatschappelijke invloeden op natuurlijke systemen en de interacties waaruit zij voortkomen;
2. de adaptatiecyclus die de voortgang beschrijft van systemen in fasen van groei en consolidatie, onvermijdelijk gevolgd door uitstoting en reorganisatie; en,
3. de topologie van netwerken en maten voor robuustheid van netwerken.

Het tweede deel van mijn proefschrift ontwikkelt de methode en het criterium in drie stappen. De eerste stap introduceert de basiskenmerken van de methode (verwijderen van soorten uit netwerken), ontwikkelt connectiviteit als een maatstaf voor netwerktopologie, en onderzoekt de geschiktheid van deze maatstaf voor het weergeven van veranderingen in robuustheid van een netwerk.

De tweede stap identificeert soorten die door verschillende vormen van menselijke invloeden risico lopen en ontwikkelt hieruit protocollen voor het verlies van soorten door het In bestaande studies over robuustheid van voedselwebben waren de protocollen gebaseerd op de verbondenheid van soorten, zonder enig verband met het risico van uitsterven. Mijn protocollen zijn getest op twee voedselwebben**.** Topologische netwerkanalyse biedt mogelijkheden voor vraagstukken met sociale predatie en verlies van habitat. Het biedt minder mogelijkheden voor emissie-gerelateerde vraagstukken zoals eutrofiëring en de invoer van gebiedsvreemde soorten. Eutrofiëring leidt tot verschuivingen in concurrentie-evenwichten tussen basissoorten. Deze vooral indirecte bron van uitsterven kan nare gevolgen hebben voor de rest van het voedselweb. Invoer van soorten vereist het toevoegen van soorten aan bestaande voedselwebben. Het toevoegen van soorten aan voedselwebben lijkt minder te maken te hebben met voedselwebtypologie maar meer met populatiedynamiek, concurrentie-evenwichten, en andere ecologische processen.

De derde stap bekijkt de manier waarop sociale en natuurlijke netwerken verbonden of gecombineerd kunnen worden zodat de wederkerige gevolgen van het verlies van soorten kunnen worden gevolgd. Ik kies voor een predatiematrix om het socio-natuurlijk netwerk weer te geven. Een predatiematrix legt vast of een overdracht van massa of energie al dan niet plaatsvindt tussen paren knooppunten in het netwerk. De matrix is vergelijkbaar met een input-output tabel, behalve dat de hoeveelheid overgedragen massa en energie niet wordt gedocumenteerd.

Topologische netwerkanalyse is toegepast op een mangrovebos in de Filippijnen. Overal in de tropen worden mangroves bedreigd met omzetting in verschillende soorten menselijk gebruik zoals aquacultuur, bosbouw en andere kustgebonden activiteiten. In deze toepassing worden verschillende ingrepen in de mangroves van Pagbilao vergeleken. Deze mangroves zijn nu in gebruik bij de lokale, arme bevolking.

Topologische netwerkanalyse omvat vier stappen: 1. constructie van een referentie sociaal-natuurlijk netwerk voor het ecosysteem en hiermee samenhangende menselijke activiteiten; 2. specificatie van alternatieve ontwikkelingspaden voor dit sociaal-natuurlijk netwerk; 3. vertaling van deze paden naar toevoeging en/of verlies van knooppunten in het netwerk; en 4. vergelijking van deze alternatieven op basis van hun verwachte gevolgen voor de robuustheid van het systeem. De laatste stap leidt tot inzichten voor het beheer.

Hoewel mijn analyse het behoud van het mangrovebos ondersteunt, identificeer ik ook mogelijke drempelwaarden voor menselijke invloed. Lokale armoede is een goede reden voor enige interventie zolang dit ten goede komt aan de lokale gemeenschap. Een mogelijkheid is conversie van ongeveer een derde van de mangroves naar aquacultuur of kleinschalige bosbouw met een adaptief beheersregiem.

Zowel de theorieontwikkeling als de toepassing bieden aanknopingspunten voor verder onderzoek. Vier van die gebieden zijn:

1. verbeterd begrip van de kwetsbaarheid van soorten voor menselijke invloeden en het vertalen van de ecologische kenmerken van soorten naar netwerkkenmerken;
2. regels voor het construeren van netwerken die zijn gebaseerd op interacties die niet bestaan uit overdracht van materiaal en energie;
3. testen van de methode op grotere gebieden met meerdere ecosystemen en meerdere sociale gemeenschappen, met ruimtelijke verbindingen tussen deze systemen; en
4. de groei van voedselwebben, het binnenkomen van soorten in ecologische gemeenschappen, en de verwording van geïntroduceerde soorten tot probleemsoorten.

Ik heb een methode en een criterium ontwikkeld voor het inschatten van toekomstige coevolutie volgend op menselijke interventie in ecosystemen. Mijn focus was hierbij op menselijke invloed, op verlies van biodiversiteit, en op plaatselijk uitsterven van soorten. Mijn methode is vanzelfsprekend niet van toepassing op alle milieuvraagstukken. Veel natuur- en milieubeheer in Nederland houdt zich bezig met herstel van habitats en de bescherming of herintroductie van soorten. Topologische netwerkanalyse heeft in deze gevallen nog niet veel te bieden omdat de topologische implicaties van het toevoegen van soorten aan netwerken nog onduidelijk zijn, en omdat de principes die ten grondslag liggen aan de ontwikkeling van habitatnetwerken onduidelijk zijn**.** Topologische netwerkanalyse biedt de meeste mogelijkheden in die gevallen waarin het te kiezen beheer afhangt van gedifferentieerde uitsterfrisico's van soorten en de mogelijkheid van een regiem verschuiving.